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TITLE OF THESIS... DEMOGRAPHY OF THE LITTLE NORTHERN CHIPMUNK EUTAMIAS MINIMUS BOREALIS (ALLEN) NEAR HEART LAKE, NORTHWEST TERRITORIES

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DEMOGRAPHY OF THE LITTLE NORTHERN CHIPMUNK *EUTAMIAS MINIMUS BOREALIS* (ALLEN) NEAR HEART LAKE, NORTHWEST TERRITORIES

by

© ROGER F. C. SMITH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

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EDMONTON, ALBERTA

FALL, 1973

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Demography of the Little Northern Chipmunk *Eutamias minimus borealis* (Allen) near Heart Lake, Northwest Territories," submitted by Roger F. C. Smith in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Zoology.

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Supervisor

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External Examiner

Date ....29 Aug 1973

ABSTRACT

Changes in a population of the little northern chipmunk *Eutamias minimus borealis* (Allen) were followed from 1967 to 1971 by means of autopsies and live-trapping on selected plots in the vicinity of Heart Lake (60° 52' N, 117° 22' W), Northwest Territories.

Pooled population size on three non-restrictive study plots (total area: 12.4 ha) declined from 71 in 1967 to 18 in 1970 and increased to 21 in 1971. Age-specific rates of natality and mortality were determined in autopsied samples and theoretical population levels were calculated that were in close agreement with real changes. Population changes were not synchronous with those of the red-backed vole *Clethrionomys gapperi*, probably because of differences in both reproductive and survival rates.

Changes in population size were caused by differences in natality during the single breeding season and by differential mortality. Potential recruitment was affected by the percentage of overwintered females which bred (from 62.5% to 84.6%), with yearling females being most variable (33% to 100%). Breeding yearling females were significantly heavier and had significantly larger cranial measurements than non-breeding females of the same age, but were not significantly different from older females.

The percentage of breeding females (from the autopsied sample) remained relatively constant (62.5% to 63.6%) with declining population size (in the live-trapped sample) until a threshold was reached that probably corresponded with the 24 minimum home ranges available. The number of embryos per female, for all breeding females, did not change within the population levels encountered within the present study.

Analysis of stomach contents showed progressive utilization of overwintered fruits, greenery, flowers and new fruits from spring to fall, although the species available from year to year depended upon vagaries of climate. Mean body weights of overwintered animals were heavier following years of good berry production. Energy requirements during the hibernation period were estimated to approximate 5,000 kilocalories and it was concluded that available energy resources necessitated hibernation. Temperatures in hibernacula were relatively stable at about 1 C in sand and 4 C in limestone substrata once the heimal threshold was exceeded.

August body weights of juveniles actively collecting seeds in cheek pouches were heavier than those of animals without seeds. "Collectors" had probably already established home ranges while the lighter "non-collectors" had not. It was proposed that "collectors" overwintered to become the heavier, breeding yearlings while "non-collectors" either failed to survive or survived on marginal home ranges to become lighter, non-breeding yearlings. During summer most non-breeding yearlings would establish home ranges and subsequently breed at two years of age.

Major theories of population regulation were incorporated into the present hypothesis which was proposed to be applicable to other small mammal populations.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
MATERIALS AND METHODS	8
Mapping	8
Live-Trapping	8
Autopsy	11
Burrows	13
Hibernation	15
Energy Available During Winter	16
Statistical Procedures	16
THE STUDY AREA	16
Live-Trapping Plots	17
Weather	20
Temperature	20
Precipitation	24
RESULTS	28
Live-Trapping	28
Comparability of results	28
Trapping success	29
Trap deaths	33
Sex ratio	35
Age structure	36

Page

Density 38

Home range 42

Movement 43

Summer loss 43

Autopsy 46

Body weights 46

Breeding season 50

Age determination 52

Sex ratio 55

Percentage breeding 56

Embryonic contribution 65

Mortality 68

Winter Strategy 74

Burrows 74

Energy requirements 77

Food 84

Winter 84

Summer 86

(i) Food available 86

(ii) Foods eaten 87

(iii) Cheek pouches 92

Weather 102

Temperature 102

Precipitation 105

General 106

Page

DISCUSSION 108

CONCLUSIONS 131

LITERATURE CITED 134

APPENDIX I 143

APPENDIX II 144

APPENDIX III 155

APPENDIX IV 156

APPENDIX V 171

LIST OF TABLES

Table		Page
1	Trap numbers and duration of trapping periods	10
2	Capture success on live-trapping plots	30
3	Numbers live-trapped and trap-deaths	34
4	Numbers of juveniles each year	37
5	Gross densities on live-trapping plots	39
6	Comparison of mean body weights of autopsied animals . .	48
7	Age classes and sex ratios of autopsied animals and breeding condition of autopsied females	49
8	Comparisons of means of various skull measurements . . .	62
9	Comparisons of mean body weights each year	64
10	Embryonic contributions from females	66
11	Ovulation rates and prenatal loss	67
12	Actual and calculated numbers of juveniles on the plots .	69
13	Age-specific survival rates	71
14	Effect of various feeding regimens upon hibernation . . .	85
15	Frequency of occurrence of various foods in chipmunk stomachs	89
16	Percentage occurrence of various seeds in cheek pouches	95
17	Calorific values of seeds found in cheek pouches	97
18	Long-term recaptures on live-trapping plots	101

LIST OF FIGURES

Figure		Page
1	Vegetative associations on live-trapping plots	18
2	Air temperatures throughout the study	21
3	Air temperatures from May to September: 1967-1971	23
4	Cumulative precipitation from April to October: 1967-1971	25
5	Snow depths at Hay River: 1966-1971	27
6	Initial captures of chipmunks for each trapping period	31
7	Number captured each year between June 20 and August 31	32
8	Home ranges of live-trapped chipmunks	41
9	Rates of disappearance of chipmunks following initial capture	44
10	Annual changes in mean body weight	47
11	Capture times of pregnant and lactating chipmunks	51
12	Percentage of population in each age group each year	53
13	Change in sex ratio with age	54
14	Percentage of females breeding at different population levels	58
15	Relationship between weight of a single testis and testis coefficient	59
16	Seasonal changes in testis measurements	60
17	Proportion of juveniles trapped and shot throughout the summer	73
18	Mean air temperatures and microclimates inside chipmunk hibernacula: winter 1969-70	76
19	Energy used by a non-hibernating chipmunk at 2.5 C	78

		Page
20	Energy used by hibernating chipmunks at various ambient temperatures	81
21	Hibernation and arousal periods in a hibernating chipmunk	82
22	Stomach contents in autopsied chipmunks: 1969-1971 . . .	90
23	Stomach contents of animals autopsied after emergence of the juveniles	94
24	Utilization of cheek pouches and occurrence of seeds in stomachs	99
25	Weight increase and use of cheek pouches by juveniles . .	103
26	Effects of precipitation and temperature on survival and breeding success	104
27	General effects of meteorological parameters on the chipmunk population	107
28	Real and theoretical population levels on the live-trapping plots	115
29	Schematic representation of the hypothesis proposed to explain changes in population levels of chipmunks	126

INTRODUCTION

Whether or not large fluctuations in population size, which have been recognized in a number of mammalian species inhabiting the higher latitudes, occur in the little northern chipmunk *Eutamias minimus borealis* (Allen) in northern Canada has not been determined. In other mammalian populations at similar latitudes a certain degree of rhythmicity has been detected in population size with a frequency of, in many cases, approximately four years and, in others, approximately ten years (Elton, 1924; Keith, 1963). Cole (1954) demonstrated a cyclic pattern evolved from random numbers and suggested that this same randomness might obtain in fluctuating populations. This suggestion was rejected by, among others, Rowan (1954) who emphasized the synchrony and repetitiveness of the peaks, and by Chitty (1960) who stated that the decline was "an association of fairly specific effects that are unlikely to follow except from fairly specific antecedents." Using a statistic gleaned from the animals themselves (body weights of adults in mid-summer), Krebs (1964) defined "cycles" of microtine abundance in terms which invalidate Cole's mathematical hypothesis. Despite difficulties in accurately enumerating these populations (see Slobodkin, 1961; Chapt. 14), large fluctuations in population size can be accepted as a reality.

Mechanisms influencing these large variations have been hotly debated for many years and a plethora of possible explanations has been suggested. Elton (1924; 1942) suggested that "climatic variations" were responsible because fluctuations in widely diverse populations were relatively synchronous. Meteorological information has not suggested rhythmicity in climatic conditions, although microenvironmental rather than meteorological

conditions are of greater importance to mammalian populations (Fuller *et al.*, 1969). A temporal restriction of climatic variation in the form of "critical periods" in conditions has been advanced by Siivonen and Koskimies (1955) and Pruitt (1957). Limitations in food supply have also been proposed, in the form of variations in quantity (Lack, 1954a), quality (Batzli and Pitelka, 1971) or specific nutrients (Auman, 1965). Intrinsic factors have been suggested in the form of stress reactions (Christian and Davis, 1964; Clulow *et al.*, 1969) or polymorphic variations in behavior (Chitty, 1967). It is possible that different mechanisms or complex interrelationships assume variable degrees of control both temporally and spatially, in which case the overall effect may well allow no factors to be distinguished as in Cole's hypothesis.

It is not known, however, whether all mammalian populations at these latitudes exhibit large fluctuations or not. This may be due to a dearth of information or to an inherent quality of stability in those populations. If such a numerically stable population does exist and is sympatric with a fluctuating one then factors influencing the parameters may aid in our understanding of population dynamics; its sharing of characteristics with either populations known to oscillate or with the more stable ones of lower latitudes may offer insights, even negatively, into factors relevant to the control of both. If the population is not stable then knowledge of any variation in size can only add to that already gained; an investigation of synchrony with sympatric species may determine which factors are of greatest importance and whether any relationship exists between these and different modes of life of the species.

The level of a population of organisms is determined, in the absence of catastrophe, both by the absolute values of its components (sex and age classes) and by the degree of interaction between many criteria (natality, mortality, longevity) which may be examined in the light of extrinsic or intrinsic factors. Intrinsic factors were not investigated in this study, the approach being based upon Wynne-Edwards (1962, p. 467) admonition that "the first hypothesis to examine as to the causes of fluctuations in animal numbers must clearly be that the instability is due primarily to fluctuations in the physical environment, and especially to those that are reflected in the availability of food." A correlative, rather than experimental, emphasis has been used throughout most of the present study.

Fuller (1969) demonstrated variation in population size in red-backed voles *Clethrionomys gapperi* and deermice *Peromyscus maniculatus* in the boreal forest of the Northwest Territories near the Heart Lake Biological Station of the University of Alberta. In that area *C. gapperi* remains active during winter (Fuller *et al.*, 1969) while *P. maniculatus* is subject to periods of torpor (Stebbins, 1971). *Eutamias minimus borealis* is sympatric with *C. gapperi* and *P. maniculatus* near Heart Lake although it has a different *modus vivendi*. The chipmunk was selected for a study of population dynamics and life habits with the major objectives of determining whether its population remains constant or varies in size and examining possible correlates with the physical environment.

Holdenreid (1940) reported that for chipmunks in general "published observations are scattered and brief, and population studies . . . have scarcely been touched," a situation which has improved only

slightly in the last three decades. Fraleigh (1929) and Hazard (1960) indicated that populations of the eastern chipmunk *Tamias striatus* remained relatively stable from year to year. Variations in population size have been recorded for the Siberian chipmunk *Eutamias sibiricus* in the Western Sayan region (Shtil'mark, 1963; 1967). A three-year study of the yellow-pine chipmunk *Eutamias amoenus* revealed only minor changes in density (Broadbooks, 1970a).

Criddle (1943) stated that in southern Manitoba *E. minimus* has "years of abundance which are followed by others of scarcity." A variation in density in this same species was shown throughout three years in Colorado by Vaughan (1969), while Sheppard (1965) found density changes in both *E. minimus* and *E. amoenus* populations in southern Alberta.

No experimental manipulation has been performed on possible causative factors, and few correlations have been suggested. Vaughan (1969) suggested that populations of *E. minimus* and other rodents in montane regions of Colorado were influenced by the timing of spring snowmelt. A relationship between size of *E. sibiricus* populations and seedfall of the stonepine *Pinus sibirica* was shown in the forests of Western Sayan, USSR, by Shtil'mark (1967).

Changes in size of home range or territory can exert a profound effect on population size by causing changes in the number of potential inhabitants for a discrete area. Martinsen (1968) showed consistent temporal changes in the size of home ranges of *E. minimus* and *E. amoenus* throughout summer with relative compatability between summers. Territoriality may or may not occur in *Eutamias* as aggressive behavior has only been recorded near the den (Gordon, 1938). Evidence from

spacing of dens and from aggression convinced Broadbooks (1970b) that *E. amoenus* was territorial and Dunford (1970) concurred with this opinion for *T. striatus* because of a reversal of dominance with distance from the den. Localized aggregations of chipmunks near abundant food supplies have been recorded (Yerger, 1953; Shtil'mark, 1967). The various biotopes available to the population must be embraced in a study of home ranges because differences in relative densities may not accurately reflect differences in density throughout the total population.

Age-specific mortality may be calculated from differences in the proportions of the population found in adjacent age classes. Postpartum development has been studied in litters of *E. amoenus* (Broadbooks, 1958), long-eared chipmunks *E. quadrimaculatus* (Wadsworth, 1969), Townsend's chipmunks *E. townsendii* (Forbes and Turner, 1972) and *E. minimus* (Forbes, 1966a). Determination of absolute age is difficult in most species and investigations of *E. minimus* are limited to that of Forbes (1966b) who used a combination of tooth eruption, tooth wear and cranial measurements to separate his population into three age groups, but gave no indications of age-specific mortalities. Shtil'mark (1967), using "tooth wear and certain other indicators" on a sample which included some animals of known age, determined how many times each individual had overwintered. He showed that a single cohort can predominate throughout several years, suggesting variation in both age-specific and annual mortalities.

The component age classes may provide differing contributions to the population within one breeding season. Differences in absolute numbers and reproductive success can also exist between consecutive years. Both Sheppard (1965) and Vaughan (1969) reported that not all

females breed as yearlings and the former noted that "considerable variation between years is apparent." No information exists concerning differences in breeding success in females of two years or older. Sheppard (1965) also found that prenatal mortality was higher in litters carried by yearlings than in those carried by older animals. A difference in the reproductive success of the population as a whole has been noted between years by Shtil'mark (1967).

Unless other factors maintain the level below that which could ever be affected by depletion of the available food resources, a population must be limited by its food supply. Food is more likely to become limiting for a monophagous or stenophagous species, but will eventually reach that stage for even the most polyphagous at high population levels. Feeding habits in chipmunks are well documented (Howell, 1929; Allen, 1938; Criddle, 1943; Tevis, 1952; Yerger, 1953; Broadbooks, 1958; Shubin, 1962; Snigirevskaya, 1964; Forbes, 1966b; and others) and may be broadly classified as opportunistic and predominantly granivorous. With the exception of Shtil'mark (1967), no correlation has been demonstrated between food supply and population levels in chipmunks, although this relationship has been shown for other species (e.g., Leopold *et al.*, 1947).

Weather is known to affect vegetative growth (Braestrup, 1940; Kalela, 1962) and to influence animals directly by means of thermal stress. If the affected vegetation is important quantitatively or qualitatively then its depletion will result in a nutritive stress on the animal population.

That thermal stress on small mammals at higher latitudes occurs

with cold weather has been known for many years. "The winter proved cold and stormy; but the quantity of snow which fell was extremely small. This circumstance was the means of ridding us of the countless swarms of mice which hitherto (1838) infested the land . . . . At present (1839) not a single one is to be seen" (Hebron, in Elton, 1942; p. 322). Chipmunks, however, are hibernators (Cade, 1963; Jaeger, 1969) and avoid the surface during the coldest period. The structure of the hibernaculum has been recorded (Criddle, 1943; Snigirevskaya, 1962), but its microclimate during winter is unknown. Broadbooks (1970b) considered hibernation to be "the safest time in the life of the chipmunk" (in central Washington) with a survival rate between October 1946 and May 1947 of 96.9%. The importance of climatic conditions in spring was emphasized by Vaughan (1969), but thermal stress in summer and fall may also play a role in the determination of survival and reproductive success.

The present study of *Eutamias minimus borealis*, then, is an attempt to determine:

1. Whether or not the population level remains constant or fluctuates in size;
2. Whether any observed changes in population size are synchronous with changes in other species of small mammals being studied in the same area;
3. Demography in the population (i.e. changes in reproductive and mortality rates between age classes and between years); and
4. A mechanism which could explain any observed changes in population levels.

MATERIALS AND METHODS

Mapping

Each of three live-trapping plots was divided into a grid pattern by the use of stakes 30.5 meters apart. This enabled capture points to be assigned reference numbers and mapped accurately.

Analysis of vegetation was conducted on each plot in 1971, species identification being determined with the aid of Moss (1959). The large grid squares were divided into smaller squares with sides 7.6 meters long and plant distribution was recorded by noting the presence or absence of each species in each small square. An estimate to the nearest ten percent was also made for each species in each small square.

Live-Trapping

Trapping was accomplished by using 23 cm x 7.6 cm x 7.6 cm aluminum Sherman live-traps. Several baits were tested in 1967 in order to obtain the best results. These included sunflower seeds, raisins, almond oil, clove oil, oil of anise, lab-chow, and peanut butter both alone and mixed with bacon fat and rolled oats, and various combinations of those baits. Traps were also set with no bait at all and with mirrors placed at the closed end. Cardboard funnels were used to test the effect of variation in entrance size. Terylene fiber insulation was placed inside traps throughout all trapping periods in order to provide protection against cooler weather. In mid-summer branches were placed over traps which were not shaded by the vegetative canopy.

As the position of the trap seemed to be more important than the bait used and the entrance size, peanut butter alone was used on unmodified traps in subsequent summers. Traps were open continuously

and were checked in mid-morning and again in late afternoon. They were moved on each plot four times at approximately monthly intervals and were generally placed on top of or at the ends of fallen logs.

One hundred traps were set each year on Plot A, while Plots B and C were investigated with 25 traps each. Distances between traps varied, but averaged approximately 5 meters. Numbers of traps and the trapping period each year are summarized in Table 1, and the numbers of traps each year in different vegetative associations on the plots are shown in Appendix I.

In 1970 and 1971, 20 of the 100 traps from Plot A were located just south of the plot in order to detect any immigration or emigration. However, all animals captured in those traps were subsequently, or had been previously, caught on the plot. The remaining two sides were bounded by convergent creeks although this probably did not provide a significant barrier because a number of natural bridges had been formed by fallen trees. The level of the creeks fell to a trickle in late summer and it is probable that no obstacle would be presented at that time. Swimming has also been recorded for chipmunks (Wilber and Weidenbacher, 1961).

All trapped animals were removed from the plots after the beginning of August 1971.

Between 7 May and 15 September 1969 a further 20 traps (total: 2,600 trap-days) were set at milepost (M.P.) 79 of the Mackenzie Highway in a small, previously-burned area of jackpine *Pinus banksiana* which was estimated by annual ring counts to be 10-11 years of age. This estimate was supported by evidence from the Mackenzie Forest Service that the area had been burned 12 years previously. In contrast to the more mature trees located on the plots, the majority of those trees bore open cones,

Table 1. Numbers of live-traps and duration of trapping throughout the study

Year	No. traps set			Date traps opened			Date traps closed			No. trap-days		
Plot	A	B	C	A	B	C	A	B	C	A	B	C
1967	100	25	25	15.vi	19.v	22.vi	24.viii	24.viii	24.viii	7,000	2,425	1,575
1968	100	25	25	11.v	12.v	12.v	25.ix	26.ix	26.ix	13,700	3,425	3,425
1969	100	25	25	1.v	30.iv	30.iv	20.x	20.x	20.x	17,200	4,325	4,325
1970	100	25	25	5.v	6.v	6.v	26.viii	27.viii	27.viii	11,300	2,825	2,825
1971	100	25	25	1.v	2.v	2.v	24.viii	25.viii	25.viii	11,500	2,875	2,875
Total trap-days										60,700	15,875	15,025

revealing a release of seeds.

Sex was determined for each captured animal by measuring the perineum. Animals were then weighed and measurements were made of hind foot, tail and ear lengths. Reproductive condition (i.e. number of nipples apparent and presence of enlarged or lactating teats) was recorded for females. Testes were generally not obvious in males. Each animal was individually marked by toe-clipping in a 1-2-4-7 combination and was released at the point of capture. Individuals obviously under thermal stress from extremes of temperature while in the traps were retained in the laboratory until they were sufficiently recovered and were then released.

In an attempt to assess the proportion of the population that was actually trapped and to attempt to locate home burrows, visible markings were placed on all individuals captured on the plots in 1968. These markings consisted of fluorescent paints sprayed on the tails, fur clipping, and dyeing the fur with Nyanzol D, Bouin's fluid and Gentian violet, as well as use of plastic collars of various colors. The collars were similar to those used for banding birds by Coulson (1963).

Females captured off the plots in early summer 1967 were maintained in cages approximately 30 cm x 60 cm x 30 cm for the duration of summer in order to determine birth dates of juveniles. Diet consisted of lab-chow and local vegetation and berries.

Autopsy

Chipmunks were collected for autopsy wherever possible, so that no temporal pattern exists in this sample. Most were shot with either a .410 shotgun or a .22 rifle, while others were snap-trapped. All animals

dying due to thermal stress during live-trapping were autopsied and added to the sample. No collection was made within 1.6 kilometers of any of the live-trapping plots.

Standard measurements were taken from all freshly-killed animals. Reproductive condition was recorded as in the live sample, and the approximate position of the testes was recorded as scrotal, abdominal or inguinal. The contents of cheek pouches were examined and the numbers of each species of seed were recorded. A small reference collection of seeds from local species, subsequently discarded, was used to determine the contents of cheek pouches. Seed identification was verified by members of the Department of Botany, University of Alberta.

Foods eaten by *E. minimus* were examined by stomach analysis. Stomach contents were identified with the aid of Dyke (1971) and by comparison with a reference collection of available foods which had been chewed by the investigator to the approximate extent of the stomach contents. Stomach weights varied widely, depending upon the time lapse from the previous meal, and were not recorded, but species composition was estimated to the nearest 10 percent.

The contents of testicular seminiferous tubules were examined at the Heart Lake laboratory by piercing testes with a scalpel and examining the tubule contents microscopically in a drop of water in order to see whether spermatozoa were present. After length and width had been measured to the nearest 0.1 mm, testes were preserved in Bouin's fluid. Seminal vesicles were designated merely as "large" or "small." In females the presence of corpora lutea, embryos or placental scars was recorded in fresh, uncleared reproductive systems which were subsequently

fixed in Bouin's fluid. Testis and ovarian weights were taken after a minimum fixation of seven days. Ovaries were embedded in paraffin wax, serially sectioned at 10 μ and stained with Harris' haematoxylin and eosin in order to count the number of corpora lutea.

Following air-drying and cleaning by dermestid beetles, skulls were measured with vernier calipers to the nearest 0.1 mm. The measurements made were total length, zygomatic breadth, occipitonasal length and interorbital breadth.

Annuli of denser bone in the lower jaw have been used for age determination in pikas (Bernstein and Klevezal, 1965; Millar and Zwickel, 1972) and in the hedgehog (Morris, 1970). These rings also appear on the labial side of the mandibular diastema of *E. minimus*, and each skull can be assigned an age based upon this criterion. Lower jaws were divided at the symphysis and one dentary was placed in R.D.O., a commercial decalcifying solution (Du Page Kinetic Laboratories Inc., Downers Grove, Ill.). After embedding in paraffin wax these decalcified dentaries were sectioned at 10 μ in the region of the diastema and stained with Harris' haematoxylin.

Burrows

Four burrows were located in sandy localities suitable for excavation after searches had been made in areas where chipmunks were known to be relatively common. A hand trowel was used to remove soil cover after a very thin suspension of Plaster of Paris had been poured into the burrow in order to trace its ramifications more accurately.

As visual tracking of animals to their burrows proved unsuccessful in 1968, radioactive tagging with Tantalum-182 wire was used in 1969

and 1970. The platinum-covered Ta-182 wire was cut into pieces approximately 3 cm long, having a radiation value of about 300 μ-curies, and was glued on plastic neck collars. These collars were not ideal in that the thickness of the neck varies during summer due to growth, at least in juveniles. A tight collar caused irritation and fur loss while loose ones tended to become snagged in foliage.

Tagged chipmunks were followed with a portable survey meter (Model 420S, Baird Atomic, Cambridge, Mass.) as the source was clearly distinguishable at a distance of 7 meters. This proved particularly useful when visual observations were obscured due to brush, stone or log obstructions, and allowed successful tracking of some animals to small areas where several possible burrow entrances were evident. Small pieces (5 cm x 5 cm) of kymograph paper smoked with oil fumes were placed against the entrances and spare traps set nearby. Recaptured animals were released at the "active" entrances, where they drew thermistors down the burrows according to the method of Hayward (1965). The only modification of Hayward's method was coating the thermistor and lead with a solution of R55 (tertiary-Butylsulphenyl-dimethyl-dithiocarbamate, Phillips Petroleum Co., Bartlesville, Okla.), a rodent repellent, in order to discourage chewing on the leads.

With the aid of a portable telethermometer (Model 42SC, Yellow Springs Instrument Co. Inc., Yellow Springs, Ohio), microclimate temperatures were measured throughout the winter of 1969-70. Five burrows were investigated - one in a sand base and four in cracks in limestone.

Four artificial burrows were constructed near Heart Lake in

summer 1969. Each had an above-ground cage which was connected by a sloping tunnel, formed from 8 cm diameter plastic pipe lined with Plaster of Paris and sand for traction, to a "nest chamber" set 25 cm below ground level. Terylene insulation was placed in a shaft between the removable lid of the subterranean box and the lid of the shaft. The shaft itself protruded above ground for approximately one meter. Two artificial burrows were set in sandy soil and two within gravel as it was not possible to set them in limestone. Thermistors were placed within the chambers so that microclimate temperatures could be recorded in these artificial overwintering sites. Visible access into each "hibernaculum" was possible via the shaft in order to detect hibernation and arousal times as well as to observe feeding periods.

Hibernation

During winter 1971-72 varying amounts of food were provided for chipmunks in a 5 C coldroom. Four male animals received maintenance food only (10 g of sunflower seeds per day); two of these animals were supplied with caches without their having to collect them while the other two were examined twice weekly to ensure that seed hoarding did not occur. A further four males received food *ad libitum*; two of these were allowed to secret a cache while the other two had all hoarded seeds removed.

Eight other chipmunks, of various ages and sexes, were placed in the same coldroom with *ad libitum* food. All animals were kept in darkness in an effort to induce hibernation. Hibernating animals were sprinkled with sawdust and examined daily in order to see whether arousal had occurred.

Using a paramagnetic Oxygen Analyser (Model F3, Beckman Instruments

Inc., Fullerton, Cal.), oxygen consumption was measured in both hibernating and non-hibernating chipmunks in laboratory coldrooms during the winters of 1970-71 and 1971-72 in order to investigate the energy needed for overwintering. The respiration chamber was placed within a darkened coldroom and connected to the analyser, which was at room temperature, by plastic tubing. Oxygen requirements for 24-hour periods were calculated for various ambient temperatures approximating those in the field.

Energy Available During Winter

Examination of the contents of cheek pouches of chipmunks in the autopsy sample indicated the probable foods stored near Heart Lake, although neither absolute nor relative quantities can be determined in this manner. Seeds of those species were collected by gathering mature fruits in summer 1971. Following washing and air drying, calorific values of the seeds were calculated using an adiabatic bomb calorimeter (Parr Instrument Co., Moline, Ill.). Both acid and sulphur corrections were performed on four replicates of each species.

Statistical Procedures

Numerous statistical texts were consulted for analysis of data, although Moroney (1951), Bailey (1959), Steel and Torrie (1960) and Sokal and Rohlf (1969) were used most commonly. Probability values of 0.05 or less were considered significant.

THE STUDY AREA

The area selected for this study of the little northern chipmunk *Eutamias minimus borealis* was located near the University of Alberta's

Heart Lake Biological Research Station (60° 52' N, 117° 22' W). The laboratory is located near the northern limit of continuous boreal forest which has been described by Rowe (1959). Maps and a physiographic description of the area under consideration are given in Fuller (1969) and Fuller *et al.* (1969).

Specimens for autopsy were collected in the forest bordering the Mackenzie Highway between Enterprise (M.P. 52) and the junction with Great Slave Lake Highway (M.P. 117), and along the latter highway to the Mackenzie River (M.P. 15), with the majority being obtained between mileposts 70 and 95 on the Mackenzie Highway.

Live-Trapping Plots

Minor variations in habitat occur throughout the boreal forest, with localized mosaics of vegetative association existing in areas of differing moisture regimes or areas of disturbance. In order to examine several of these habitats three plots, designated A, B, and C were established for live-trapping at the beginning of the study in 1967.

Plot A (Fig. 1) is an irregular but roughly triangular area of 6.4 ha (15.8 acres) with a slight slope toward the northeast situated between two confluent creeks at M.P. 85 of the Mackenzie Highway. Near the confluence is a small gravelly bar covered with sparse black spruce *Picea mariana*, but subject to occasional spring inundation. Further from the creek the plot is typical muskeg with black spruce and larch *Larix laricina* and an understory of Labrador tea *Ledum groenlandicum* and mosses *Sphagnum* spp. and *Hylocomium splendens*. A sandy rise towards the southwest is dominated by jackpine with invading white spruce *Picea glauca* and a shrub layer of predominantly buffaloberry *Shepherdia*

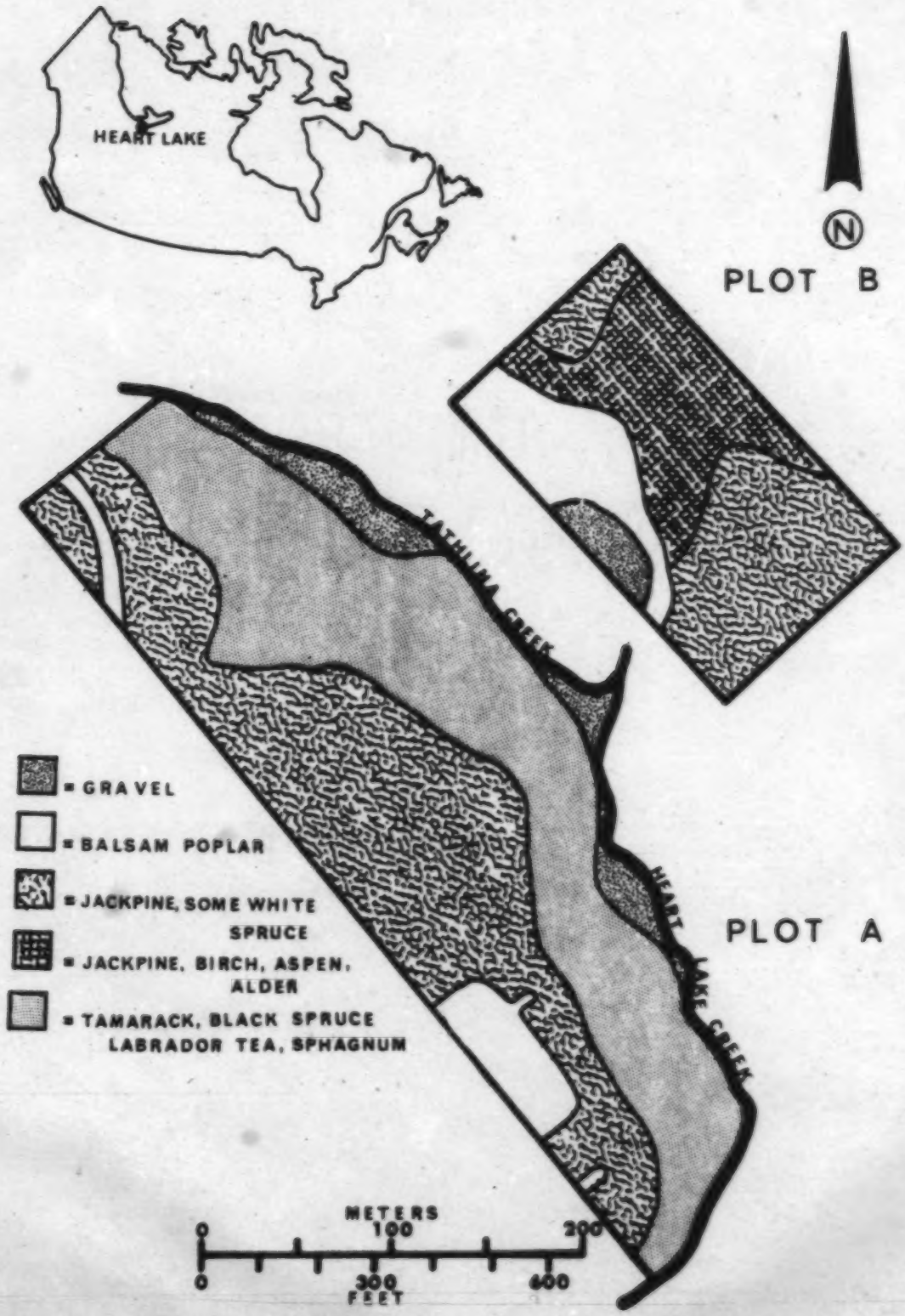


Figure 1. Vegetative associations on live-trapping plots.

canadensis, wild rose *Rosa acicularis* and shrubby cinquefoil *Potentilla fruticosa* with some juniper *Juniperus communis*. Bearberry *Arctostaphylos uva-ursi*, bog cranberry *Vaccinium vitis-idaea* and bastard toadflax *Geocaulon lividum* with some lichens *Cladonia* spp. dominate the forest floor. Disturbed parts of the sandy rise are generally occupied by small balsam poplar *Populus balsamifera* and wild rose with bearberry, bog cranberry and grasses *Calamagrostis* spp. covering much of the ground.

Plot B (Fig. 1) is 2.6 ha (6.4 acres) in size, and is set on an area of limestone gravel overlain by topsoil between 10 and 60 cm (4 – 24 in) in depth. It is located at M.P. 82 of the Mackenzie Highway. Approximately one-third of the plot, which has a slight southwest slope, is covered by jackpine with invading white spruce and is similar to the drier parts of Plot A or to Fuller's (1969) Plots V and VB. A further third is covered with a mixed canopy of jackpine, white spruce and aspen *Populus tremuloides*, with occasional birch *Betula papyrifera*. Most of this portion has a dense understory of alder *Alnus crispa* with some high bush cranberry *Viburnum edule*, buffaloberry and wild rose. The forest floor here is well covered by alpine bearberry *Arctostaphylos rubra*, bearberry and bog cranberry. The final third of Plot B has been quarried for limestone and contains balsam poplar with occasional grasses, bearberry and wild strawberry *Fragaria virginiana*.

Plot C, of 3.4 ha (8.3 acres), is located on a flat area near the Heart Lake Fire Tower and has up to 10 cm (4 in) of topsoil overlying solid limestone. The plot, which is largely embraced by that used to study the red squirrel *Tamiasciurus hudsonicus* (Zirul and Fuller, 1971), has a fairly open canopy of jackpine with occasional alder and juniper

in the shrub layer. Scattered clumps of *Sphagnum* spp., *Cladonia* spp. and bearberry occur where moisture and soil permit growth. Most of the plot was similar to Zirul's (1970) landscape classification of "semi-open dry."

Weather

Temperature

Maximum and minimum air temperatures were recorded daily throughout the study from a shaded thermometer approximately five feet above soil surface near the laboratory. Means of average daily temperature for 10-day periods (1-10; 11-20; 21-end of month) are shown in Figure 2. Temperatures throughout the winter of 1966-67 are recorded in Fuller *et al.* (1969). Data are missing for the last period in December 1967 and for January 1968, but the coldest winter during the study, in terms of air temperature, seems to have been 1968-69. Spring temperatures (early May) were lowest in 1967 and 1968 and warmest in 1969, while autumn temperatures did not plunge significantly in any of the years.

Provided that sufficient insulation in the form of snow cover is maintained during the coldest months (when the animals are in hibernacula), chipmunks are probably influenced more by air temperatures during their period of activity. The active period usually lasts from approximately mid-April until mid-October and hibernacula probably could provide protection during cold spells for several weeks immediately following and preceding hibernation.

Means of daily average air temperatures for 10-day periods from May to September are shown in Figure 3. The mean temperature for those five months was lowest in 1968 (10.1 C, 50.1 F) and highest in 1971 (13.9 C, 56.9 F). Means for May, the period of greatest plant growth,

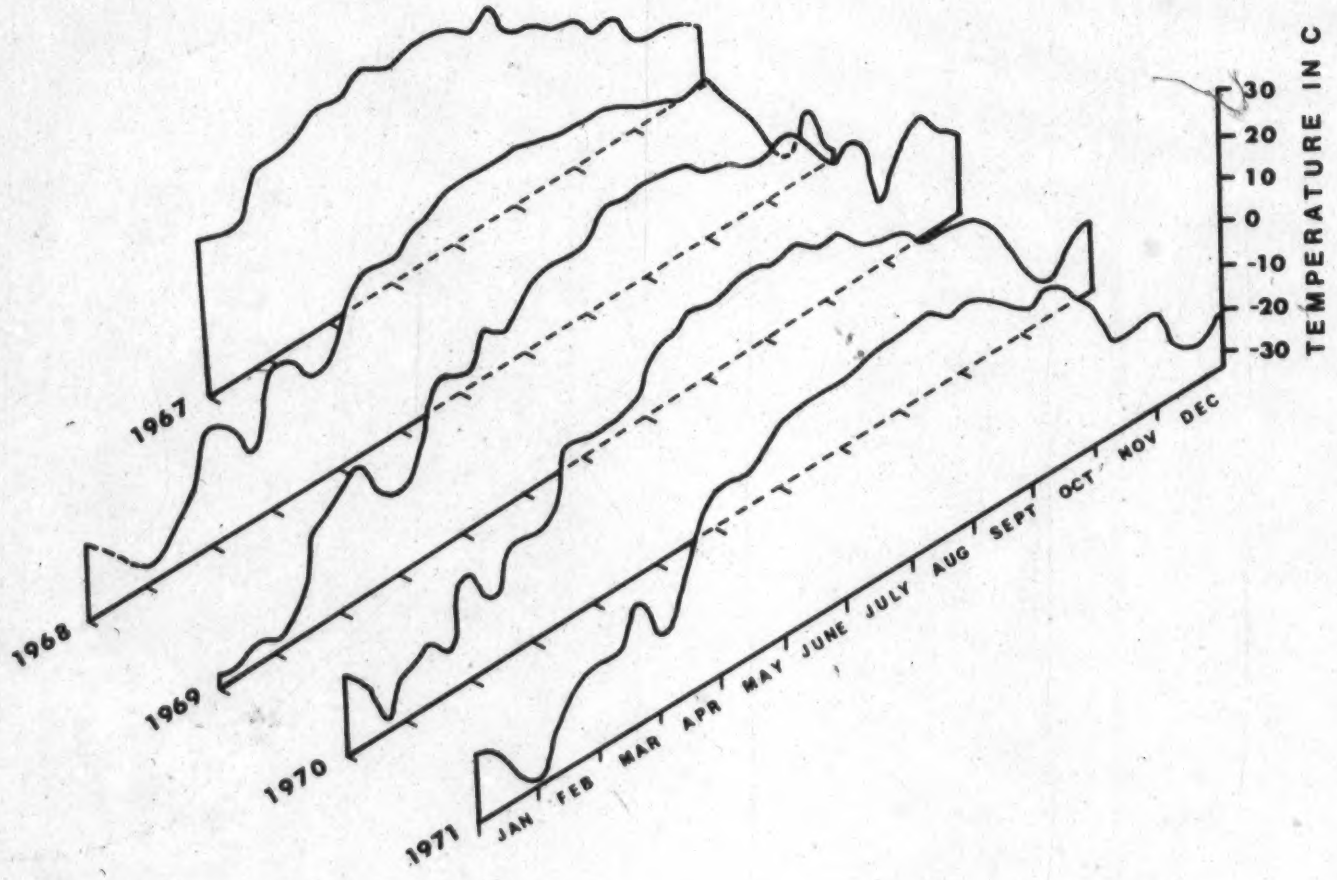
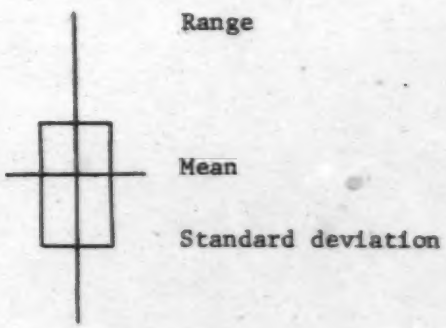
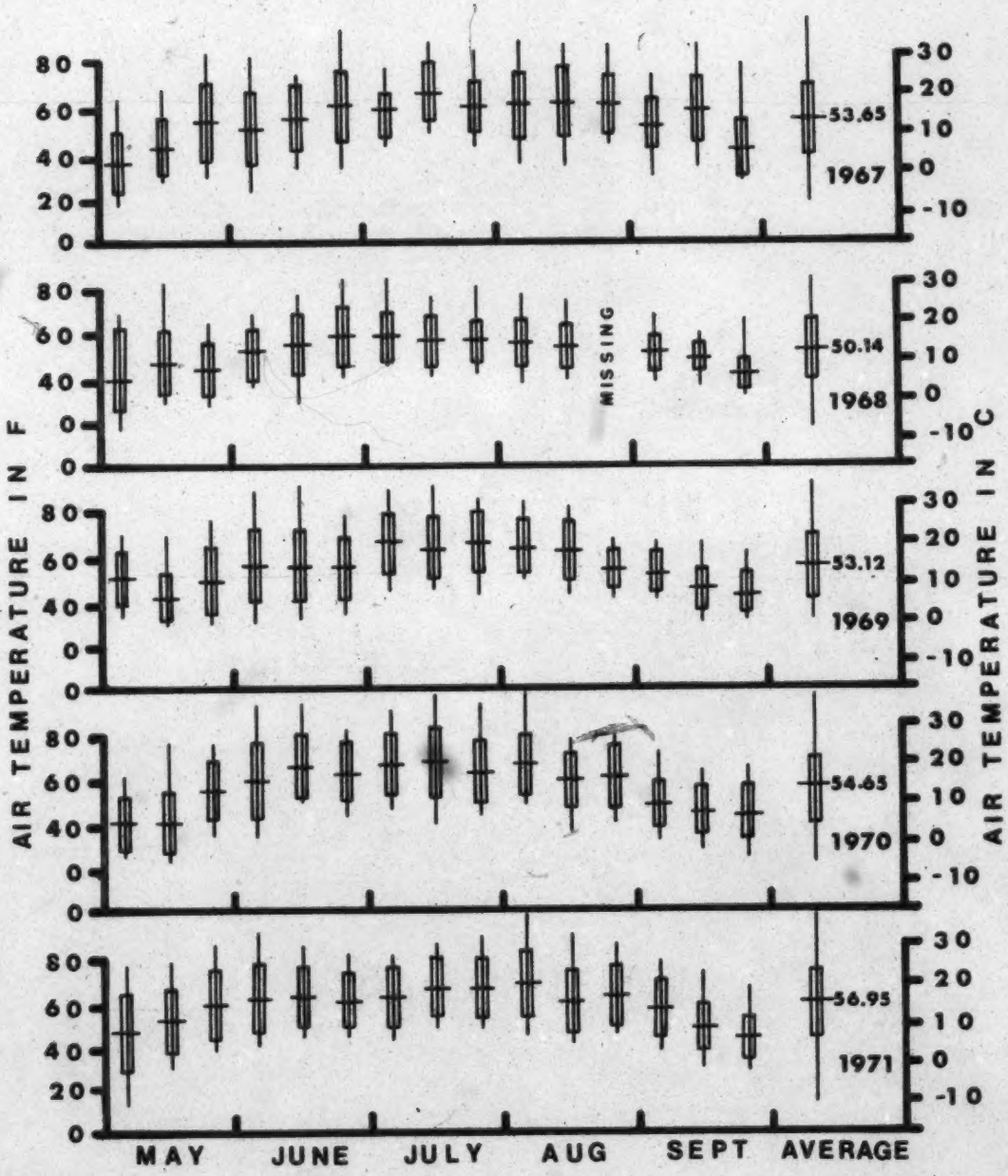


Figure 2. Means of 10-day (1-10; 11-20; 21-end of month) air temperatures recorded at Heart Lake Laboratory throughout the study.

Figure 3. Bar diagrams illustrating range, standard deviation and mean of air temperatures measured at Heart Lake laboratory. Ten-day periods (1-10; 11-20; 21-end of month) from May to September are shown.




AIR TEMPERATURE IN F
AIR TEMPERATURE IN C
80
60
40
20
0
30
20
10
0
-10
53.65
1967
MISSING
50.14
1968
53.12
1969
54.65
1970
56.95
1971
MAY
JUNE
JULY
AUG
SEPT
AVERAGE

were 5.8 C (42.5 F) in 1967, 4.9 C (40.8 F) in 1968, 7.3 C (45.2 F) in 1969, 6.7 C (44.0 F) in 1970 and 10.5 C (50.9 F) in 1971. Spring was delayed in May 1967 (see also Fuller *et al.*, 1969) and was coolest in 1968 which was then followed by the coolest summer. The warmest spring occurred in 1971 and was followed by the warmest summer during the study (Figs. 2 and 3).

Precipitation

Records of precipitation at the laboratory were sporadic and those shown for April-October (Fig. 4) are converted into 10-day totals from observations at Hay River (Paradise Gardens) (Environment Canada, 1967-71). The moderating influence of Great Slave Lake on the climate of Hay River has been discussed by Fuller (1969), and records from Paradise Gardens (16 miles south of the lake) were considered to more nearly approximate those near Heart Lake.

In 1967 and 1968 most precipitation fell in mid-summer following relatively dry spring periods (Fig. 4). Both spring and summer were dry in 1969, with little precipitation until late August. After heavy spring storms which deposited a lot of moisture in the soil, both 1970 and 1971 had dry summers.

It can be deduced that the growing period for vegetation was best in 1970 and, to a slightly lesser extent, in 1971, with both warm temperatures and plentiful soil moisture, while spring in 1967, 1968 and 1969 was drier and cooler. The fruiting period (July and early August) was cool and wet in 1967 and 1968, warm and dry in 1969, and warm with moderate moisture in 1970 and 1971.

The insulative value of snow cover for small mammals has been

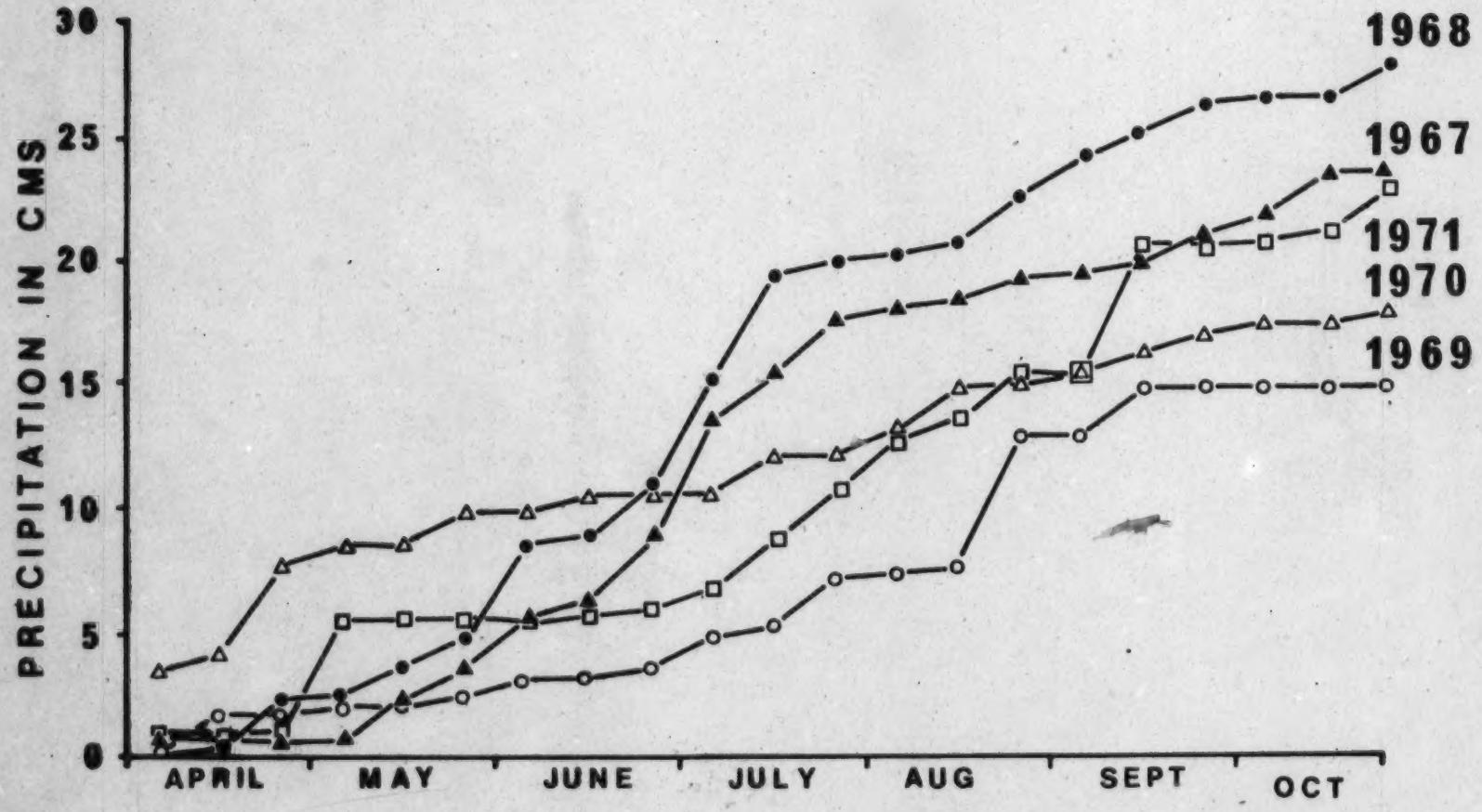


Figure 4. Cumulative precipitation at Hay River (Paradise Gardens) from April to October each year. Data for September 1967 are missing and figures from Hay River (Airport) were used for that one month. Snow depths in spring and fall have been converted to centimeters of water.

stressed by, among others, Formozov (1946), Coulianos and Johnels (1962) and Fuller *et al.* (1969). Insulation of this type may not be as important for chipmunks as it is for mammals like *Clethrionomys* which are active all winter (Stebbins, 1971), but could conceivably affect the temperature in the hibernaculum. Snow depth was measured on Fuller's (1969) Plot I which, at M.P. 83.6 of the Mackenzie Highway, is approximately midway between Plots A and C in this study (Fig. 5). Because the station was unoccupied in 1967-68, figures from the Hay River airport (Environment Canada, 1967-71) have been used for that winter. Lack of snow measurements at Paradise Gardens necessitated use of the Hay River data.

Snow depth at the end of each month is roughly the same for Hay River and the Heart Lake area (Fig. 5). A considerable difference occurs between years, with a deep snow cover for the coldest months of winter 1966-67, a smaller amount in the winters of 1967-68 and 1968-69, and a shallow cover in 1969-70 and 1970-71. The "heimal threshold" of about 20 cm (Pruitt, 1970) was exceeded by the end of October in 1966, the end of November in 1967, 1968 and 1969, but not until the end of December in 1970.

Temperature at the soil surface was monitored near the Heart Lake laboratory for each winter except 1967-68 by the method outlined in Fuller *et al.* (1969). The lowest subnivean temperature in winter 1966-67 was -9 C (16 F) (Fuller *et al.*, 1969). In 1967-68 there was "no snow until the end of October" (William Clark, pers. comm.) and only 18.5 cm by December 6, 1967, so that a poor insulative snow blanket can be assumed in early winter. Insulation was probably better in 1968-69,

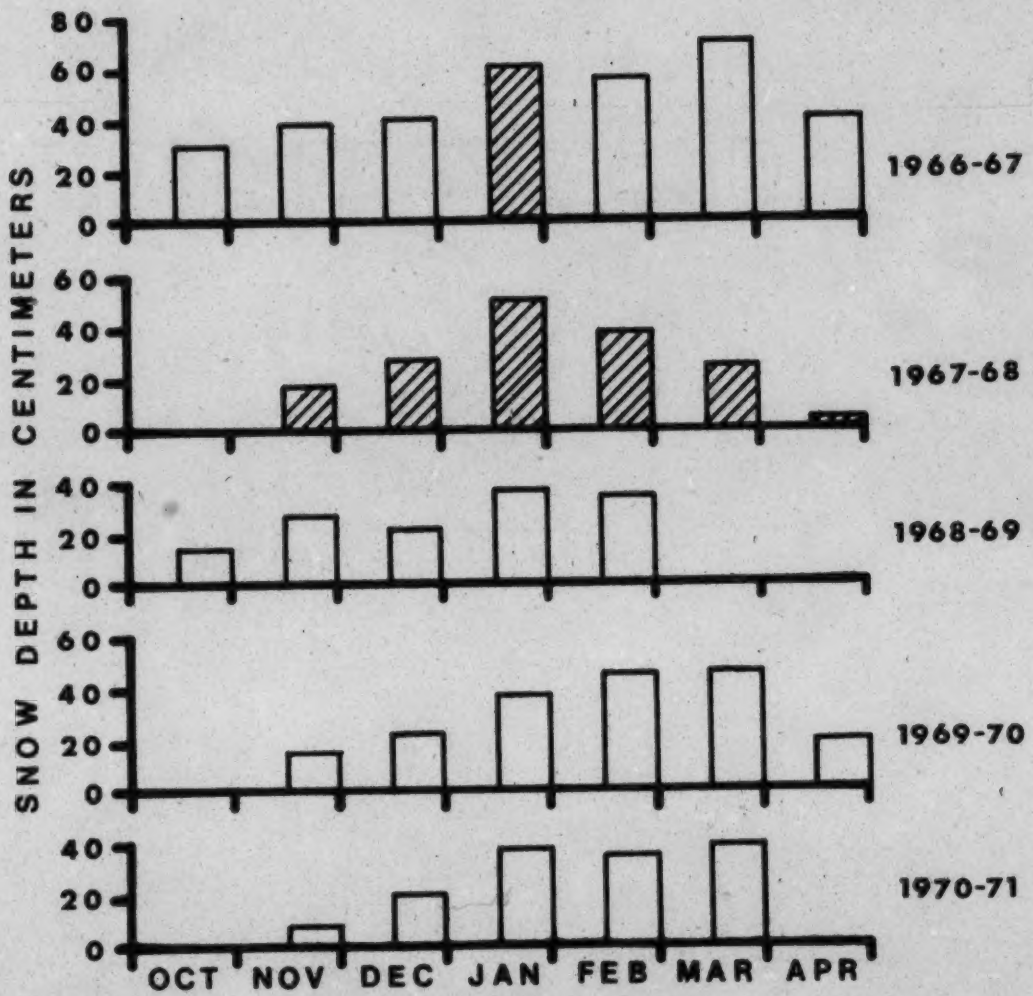


Figure 5. Snow depth at the end of each month at Hay River (Airport) (hatched bars) and on Fuller's (1969) Plot I (open bars). Values for winter 1967-68 on Plot I are adapted from Fuller *et al.* (1969).

with a minimum subnivean temperature of -14 C (7 F), and in 1969-70 when the minimum was -12.5 C (9.5 F). Snow depth in 1969-70 was relatively low, but air temperatures (Fig. 2) were generally mild. In winter 1970-71 snowfall was very light and the minimum subnivean temperature was -19 C (-2 F). Minimum subnivean temperatures were measured every two weeks on Fuller's (1969) Plot I and were generally slightly lower than those monitored at the laboratory although annual differences were similar to those near the laboratory: -9 C in 1966-67, -18 C in 1968-69, -15 C in 1969-70, -24 C in 1970-71. In 1970-71 the minimum subnivean temperature was recorded on December 1, before the heimal threshold was exceeded, whereas in other years the minima were recorded at the end of January or in mid-February when the heimal threshold had been exceeded. Winter insulation, then, seems to have been best (warmest) for sibnivean animals in 1966-67, moderate in 1968-69 and 1969-70, and poorer in 1970-71 and, probably, 1967-68.

RESULTS

Live-Trapping

Comparability of results

Sightings of marked animals on the plots were too infrequent for an accurate determination of the percentage of the population caught in traps. However, as sightings of unmarked animals fell to zero and as no new animals were captured at the extremities of the trapping periods, it would appear that at least a very large proportion of the population was trapped and marked.

The duration of trapping was not consistent (Table 1) so that

differences in numbers trapped each year could be a consequence of the period of trapping. Initial captures within 10-day periods throughout the five summers were most common in late July and early August (Fig. 6). In 1968 and 1969 trapping extended beyond the time spans shown, although no new animals were captured.

The only time span common to all years is the period (taken to the nearest 10-day division) from June 20 to August 31 (10,800 trap-days). The numbers of animals trapped each year within this 72-day period are shown in Figure 7, as are the total numbers trapped each year. Chi-square tests between points for each year show that the total numbers of chipmunks trapped for each year are not significantly different from the numbers trapped each year between June 20 and August 31. Actual numbers trapped, then, result from a real difference in trapping success and not from a difference in the periods trapped.

Trapping success

Considerable variation in trapping success, including both initial and total captures on each plot, was encountered both between years and between plots (Table 2). From a high of 71 individual animals in 1967, the pooled population on the plots declined to a low of 18 in 1970 before recovering slightly in 1971. The average number of individuals captured per 100 trap-days varied from a minimum of 0.106 in 1970 to a maximum of 0.645 in 1967.

Plot B allowed the greatest success in trapping (although not the highest population for the whole plot), followed by Plot C and Plot A. These differences are probably due to the different numbers of traps used on the different plots as well as to physiographic dissimilarities

Table 2. Capture success on the live-trapping plots throughout the study

Year	No. captured				No. individuals per 100 trap-days			Total captures per 100 trap-days			Average no, captures per chipmunk		
Plot	A	B	C	Total	A	B	C	A	B	C	A	B	C
1967	38	21	12	71	0.543	0.864	0.762	0.700	1.897	0.762	1.289	2.190	1.000
1968	32	17	4	53	0.234	0.496	0.117	1.131	1.577	0.146	4.844	3.176	1.250
1969	9	7	12	28	0.052	0.162	0.277	0.151	0.393	0.693	2.889	2.429	2.500
1970	6	8	4	18	0.053	0.283	0.142	0.124	0.460	0.142	2.333	1.625	1.000
1971	13	7	1	21	0.113	0.248	0.035	0.122	0.283	0.035	1.077	1.143	1.000
Total	98	60	33	191	0.161	0.378	0.220	0.425	0.869	0.346	2.633	2.300	1.576
Total captures	316	145	58	519									

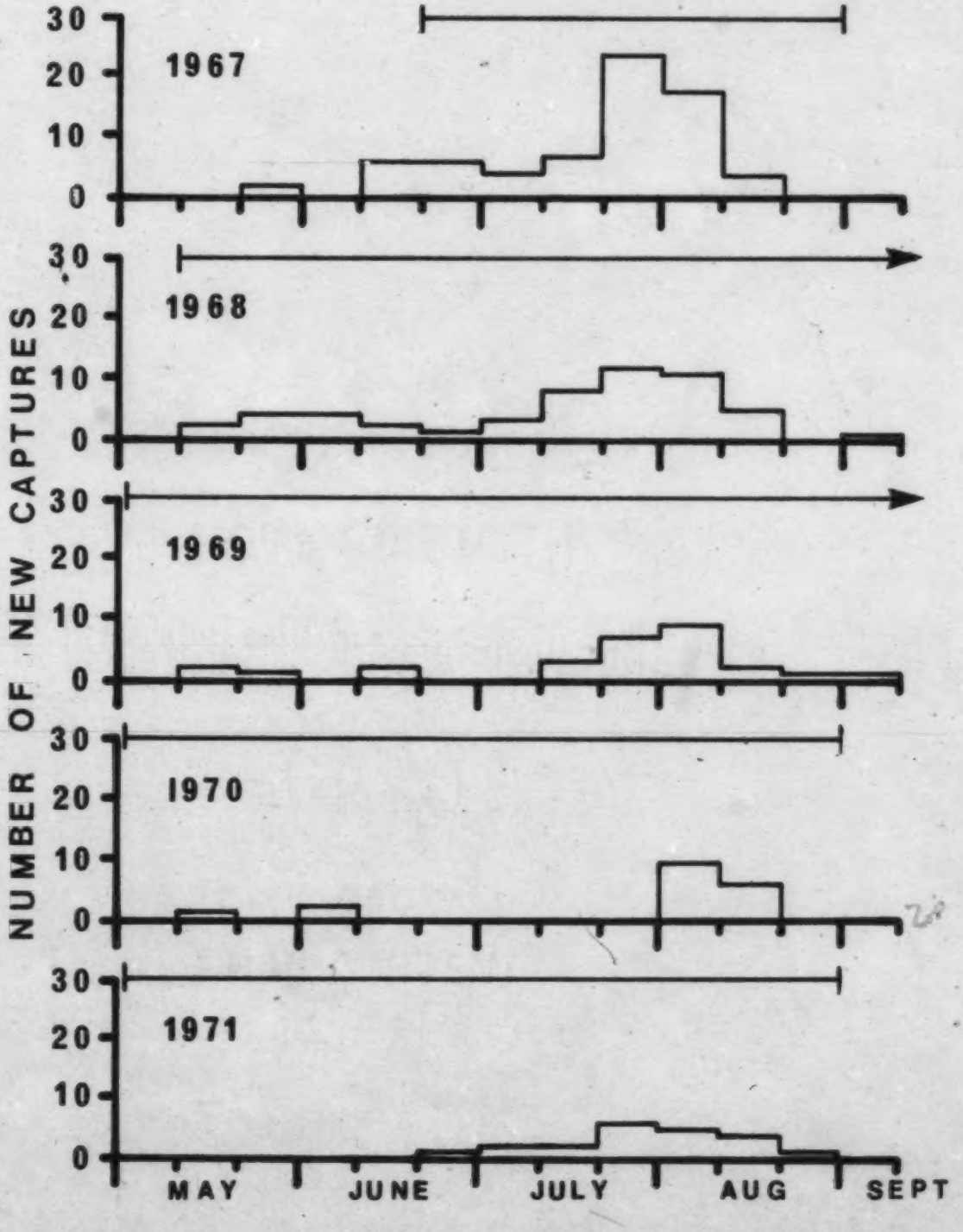


Figure 6. Numbers of individual chipmunks captured for the first time, in 10-day periods (1-10; 11-20; 21-end of month) throughout five years. Horizontal lines represent the time spans when all three plots were being trapped. Trapping continued beyond September 10 in 1968 and 1969.

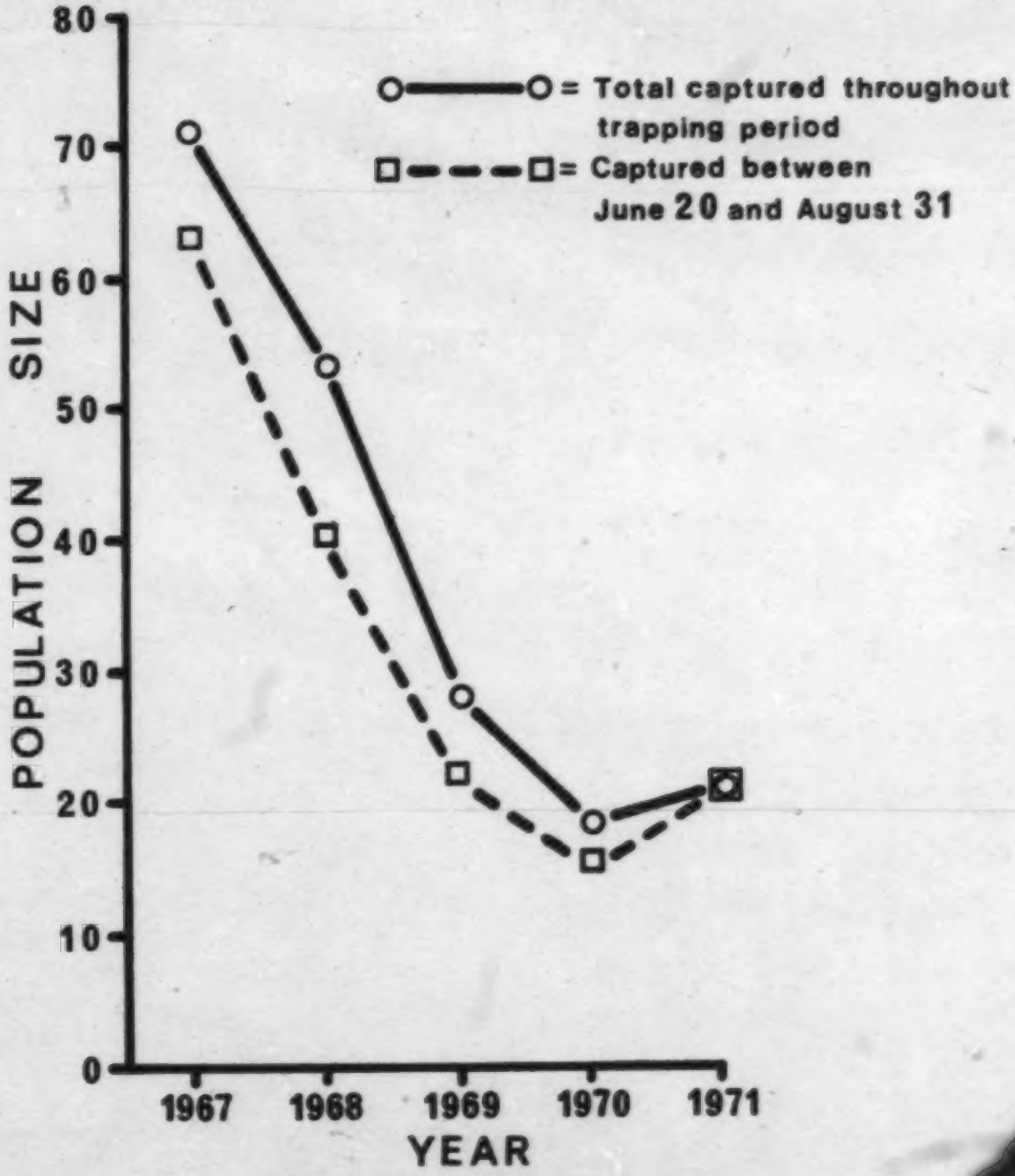


Figure 7. Total numbers captured on all three live-trapping plots (unbroken line) and numbers captured each year between June 20 and August 31 (broken line).

between the plots. The two smaller plots (B and C) probably had a greater proportion of non-residents included in their total numbers of captures as these two plots were considerably smaller than Plot A and none of the plots had restrictive boundaries.

The average number of captures per individual was generally higher on Plots A and B (3.22 and 2.42 respectively) than on Plot C (1.76). Excluding those animals captured only once, the average number of captures per individual was 5.11 on Plot A (N = 53), 4.04 on Plot B (N = 28) and 1.92 on Plot C (N = 12). The proportion of transients in the population was apparently greater on Plot C, whereas slightly more residents were captured on Plot A than Plot B. Plot A is almost 2.5 times larger than Plot B and the difference between the average number of captures on these plots may be caused by a larger proportion of captures on Plot B of animals from outside the plot but which have home ranges only very occasionally allowing capture within the plot's boundaries. Plot C was set on a limestone substratum and possibly a lack of suitable sites for burrow formation prevented an abundance of permanent residents, although the food supply would have been expected to attract some transients.

In 1969 no chipmunks were captured during 2,600 live-trap-days in an area of young, seed-releasing jackpine near Heart Lake, suggesting that the population here was no higher than, and, possibly, lower than in areas of no seedfall such as Plots A, B and C. Trapping was conducted in that area because jackpine is known to produce a variable seedfall with larger crops every three to six years, although no seeds are released, while younger trees release seeds every year (Crossley, 1956;

Table 3. Summary of total numbers, sex ratios and trap-deaths of chipmunks live-trapped on the study plots. The numbers in parentheses refer to deaths in the traps

Year	♂♂	♀♀	Total	% trap-death	Probability*
1967	35	36	71		N.S.
	(1)	(5)	(6)	8.4	
1968	35	18	53		<0.025
	(8)	(3)	(11)	20.8	
1969	18	10	28		N.S.
	(6)	(3)	(9)	32.1	
1970	10	8	18		N.S.
	(4)	(3)	(7)	38.9	
1971	14	7	21		N.S.
	(7)	(2)	(7)	33.3	
Total	113	78	191	20.9	
	(26)	(16)	(42)		

*Sex ratios compared by X^2 test.

Anonymous, 1965). The very low numbers of animals captured in 1969 probably obscured any meaningful results but seedfall from the trees would not appear to influence population size near Heart Lake although such is thought to be the case in the Siberian chipmunk (Shtil'mark, 1967). However, those seeds are much larger than the ones on the trees near Heart Lake.

Trap deaths

A large proportion (which ranged from 8 to 39 percent) of live-trapped chipmunks died either in the traps or as a consequence of trapping (Table 3). This mortality was due to thermal stress and occurred mainly in early spring and late autumn when terylene inside the traps provided insufficient insulation (Appendix II). However, several deaths occurred in mid-summer when branches providing shade were blown away so that the trapped animals died of heat prostration. The effect of this mortality on population levels on the plots in subsequent years is discussed in a later section.

Sex ratio

Except for 1968, when a significant excess of males was trapped, sexual parity was observed in live-trapped animals (Table 3). Males were captured more frequently than females in all years except in 1967 when the numbers were almost equal. Male rodents are generally considered to be more exposed to trapping and shooting because they normally travel greater distances than females and at certain times of the year (e.g. during lactation) are more active than females (Stickel, 1954; Beer *et al.*, 1958), so that some disparity favoring the capture of males is to be expected. However, the large difference in 1968 can not be

attributed entirely to a trapping bias because of consistency in trapping from year to year.

If captures in 1968 are analysed for each plot separately a difference in sex ratio is apparent. Plot A produced a total of 10 females (3 adults; 7 juveniles) and 22 males (8 adults; 14 juveniles). Plot B produced four females (3 adults; 1 juvenile) and 13 males (4 adults; 9 juveniles) and Plot C produced four females (2 adults; 2 juveniles) but no males. A change in age structure of the population, provided that sex- and age-specific mortalities both apply, could alter the sex ratio. Juveniles comprised 62% of the live-trapped sample (Table 4), a figure no higher than in other years. Plot A had 67.5% juveniles and Plot B 58.8%, while 50.0% of the captures on Plot C were juvenile. Thus, unless the sex ratio in juveniles was heavily biased toward males, the difference would not be due to a change in age structure.

The greatest percentage of males in 1968 was captured on Plot B (75.6%), with 68.8% on Plot A and no males on Plot C. If food was in better supply on Plots A and B, males would probably tend to congregate there to a greater extent than females because of their generally greater mobility. Another possibility is that overwintering survival was higher, especially in males, on Plots A and B.

Age structure

Juvenile chipmunks first appeared in the traps each year in mid-July (Appendix II). Growth was rapid and hind foot, tail and ear lengths quickly approached those of overwintered animals so that, by late summer, such measurements were of no value in determining age. On the basis of body weight and head size, however, it was possible to

Table 4. Number and percentage of juveniles (by weight) on live-trapping plots throughout the study

Year	Number of juveniles			% juveniles	Number of adults			Total		
	♂	♀	Total		♂	♀	Total	♂	♀	Total
1967	25	19	44	62	10	17	27	35	36	71
1968	23	10	33	62	12	8	20	35	18	53
1969	13	6	19	68	5	4	9	18	10	28
1970	8	5	13	72	2	3	5	10	8	18
1971	11	3	14	67	3	4	7	14	7	21
Total	80	43	123	64	32	36	68	112	79	191

separate animals which had not overwintered (i.e. juveniles) from those which had overwintered once or more, although weight changes throughout summer allowed no single separation point. Age determination of overwintered animals was not possible in the live-trapped sample and all of these were classified as adults.

The proportion of juveniles in the live-trapped population varied slightly each year with a slight increase in 1970 and, to a smaller extent, in 1971 (Table 4). This could suggest that either breeding success or the survival of very young animals was higher in the last two years of the study.

The percentage, although not the actual number, of live-trapped juveniles increased with decreasing population size, although that correlation was not statistically significant (Spearman's coefficient of rank correlation $R_s = -0.825$; $t = 2.528$; $0.05 < P < 0.10$). Similarly, there was no statistically significant difference in the ratio of juveniles to adults in any year. Data are scant so that the exact nature of any relationship remains equivocal, but an indication exists (Table 4) that a threshold, above which juvenile presence does not decline further, may occur at a total population level of 20-30. Conclusions inferring density-dependance on the basis of correlation, however, must remain suspect (Eberhardt, 1970).

Density

As was shown in terms of trapping success (Table 2), Plot B appears to have been the type of habitat best suited to chipmunks and was subject to least fluctuation in gross density (Table 5). In general, Plot B contained a younger successional stage and displayed the greatest

Table 5. Gross density of chipmunks captured on the study plots. Plot A' refers to that portion of Plot A covered by a jackpine-white spruce association

Year	Number of animals per hectare				
	Plot A (6.4 ha)	Plot A' (3.0 ha)	Plot B (2.6 ha)	Plot C (3.4 ha)	Total (12.4 ha)
1967	5.9	12.7	8.1	3.5	5.7
1968	5.0	10.6	6.5	1.2	4.2
1969	1.4	3.0	2.7	3.5	2.3
1970	0.93	2.0	3.1	1.2	1.5
1971	2.0	4.2	2.7	0.3	1.7
Average	3.04	6.50	4.62	1.94	3.06

floral diversity as well as possible edge effects, so that a greater production of chipmunks was not unexpected. Non-limiting boundaries on all plots almost certainly allowed recapture of non-resident animals, especially on the smaller Plots B and C, so that estimates of gross density are probably inflated, but comparisons of pooled data between years should show a relative error allowing comparison to be made.

Much of Plot A proved to be habitat unsuitable for chipmunks and all animals captured were found in the area of jackpine-white spruce or on the early successional areas (balsam poplar) with only occasional captures being recorded in the black-spruce sphagnum section by individuals which were previously captured in jackpine. Jackpine covered approximately half (3.04 ha, 7.52 acres) of Plot A, and that portion supported a density usually greater than either of the other two plots (Table 5). Plot B was considered to be too small to be subdivided in terms of vegetational differences and no definite preference for any section of the plot was found in captures (Appendix II).

A certain amount of variation exists between habitats. The jackpine-white spruce community was normally best, with mixed jackpine-white spruce-aspen-birch supporting a lower density of chipmunks. Densities in the jackpine-alder-juniper community (Plot C) were usually lowest. However, in 1969 Plot C supported the greatest density and also had an increased temporal occupancy--an average 2.5 captures per chipmunk versus single captures in most other years (Table 2).

The density in the jackpine-white spruce half of Plot A was exceeded by that on Plot B only in 1970. This increase was probably due to an abundant crop of berries (particularly buffaloberry) on Plot B in that year.

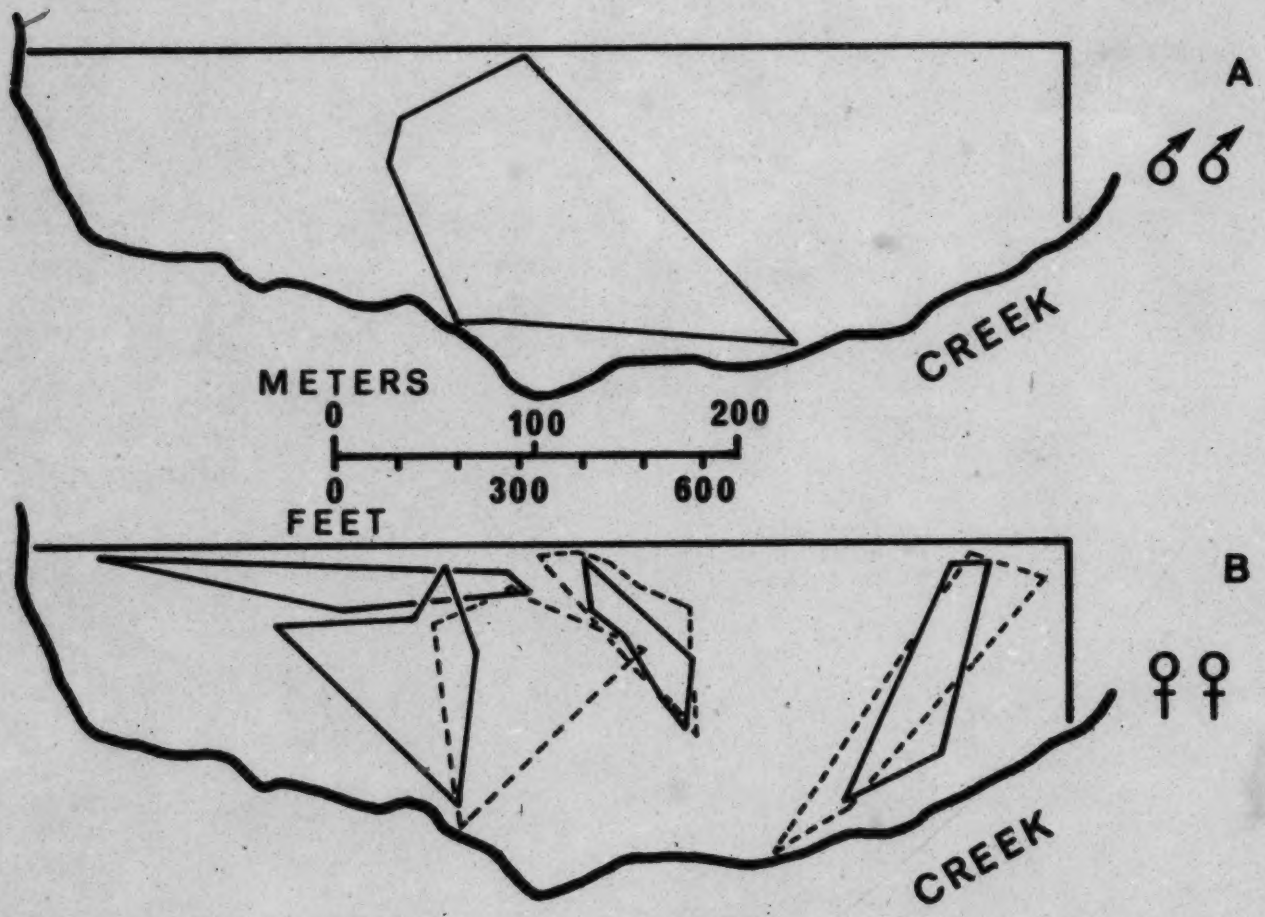


Figure 8A. Minimum home range of an adult male chipmunk (unbroken lines) on Plot A in 1967.

B. Minimum home ranges of adult (unbroken lines) and juvenile (broken lines) female chipmunks on Plot A in 1967.

Differences between years reflect the general decrease in population size from 1967 to 1970 and the slight population increase in 1971.

Home range

Estimates of home range should be based upon 15 to 20 captures (Broadbooks, 1949), although Sheppard (1972) used a minimum of only five. Recaptures in the present study were infrequent (average: 2.72 captures per chipmunk) so that an accurate determination of home range was not possible.

Only four adult females were captured three or more times on Plot A in 1967 and those females had minimum home ranges of 0.5, 0.3, 0.1 and 0.3 hectares (average: 0.3 ha, 0.7 acres) (Fig. 8B). Some overlap of ranges occurred, while other females had single captures or one recapture within these home ranges; the ranges would thus appear to have undefended borders. A single female minimum home range of 0.8 ha (2.0 acres) could be determined in 1968 on Plot B. One adult male minimum home range (1.5 ha, 3.8 acres) could be calculated in 1967, and other males were captured within that area (Fig. 8A). Holdenreid (1940) also found that males tended to move over greater distances than females and Broadbooks (1970b) found adult male home ranges averaging 1.62 hectares in *E. amoenus*.

Three juvenile females were trapped three or more times in 1967 and their minimum home ranges (0.6, 0.2 and 0.4 hectares; average 0.4 ha, 1.0 acres) were slightly larger than those of adult females and followed their general outlines but extended the borders (Fig. 8A). Juvenile males seemed to move long distances, but no minimum home range could be calculated.

Movement

One female first trapped as a juvenile on Plot A in 1968 was recaptured off the plot 1.6 kilometers from the original capture point as a breeding adult in 1970. Other individuals were recaptured on the plots after being absent for more than one year or, in one case, two years. Animals were not trapped in the same locality in subsequent years, suggesting that movement to a new home range may occur each year.

Immigration and emigration may occur during the summer, but as all chipmunks captured in the 20 traps just off Plot A were subsequently, or had been previously, caught on the plot, definite unidirectional movements could not be determined. All animals were removed from the plots in August 1971 and an extensive examination prior to snowmelt in spring 1972 revealed that three animals had resettled Plot A. As the snow was approximately 60 cm deep when the chipmunks were collected, immigration probably occurred before winter 1971-72, so that successful resettlement of an area can probably occur in fall. Age-determination (see later) proved that these three animals were yearlings, so that they probably resettled the plot when juvenile.

Summer loss

The length of time following initial capture during which adults and juveniles (summed over all years) were known to be alive (i.e. were recaptured) (Appendix II) was calculated (Fig. 9). More juveniles than adults were present in the sample, so that both actual numbers and the disappearance from calculated populations of 100 initial captures of are shown. Most juveniles and approximately half the adult chipmunks were captured only once so that the rate of loss from the plots was extremely

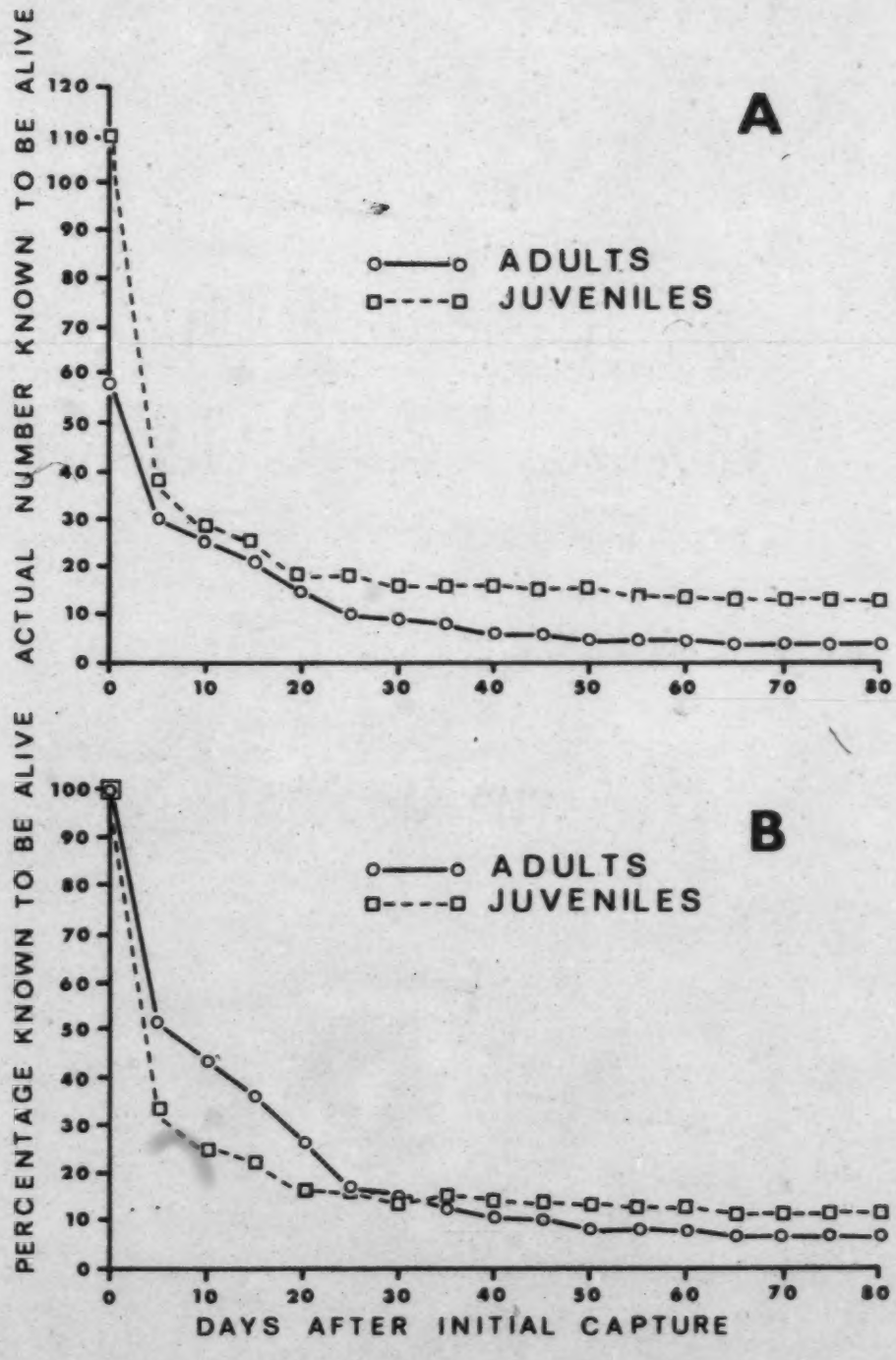


Figure 9. Actual numbers (Fig. 9A) and percentage (Fig. 9B) of adults (unbroken line) and juveniles (broken line) known to be alive at various intervals following initial capture and release.

high in the first few days.

Juveniles appear to have been lost (i.e. to have died, emigrated or not been recaptured) at a faster rate than overwintered animals. There is no reason to suppose a difference in trappability between juveniles and adults as no summer torpor was observed in captive animals. The greater disappearance rate of juveniles must have been caused by either a greater mortality, an increased emigration rate or an increased proportion of occasional captures of animals from outside the plots themselves. The mean time of occupancy of the plots was 6.10 days in adults and 1.35 days in juveniles. A X^2 test of independence (Steel and Torrie, 1960) had a value of 10.67, showing that adults remained on the plots significantly longer than juveniles.

Mean times of occupancy of all chipmunks on the plots, calculated for each year except 1971 when removal of all animals invalidated this analysis, were: 1967, 4.37 days; 1968, 8.41 days; 1969, 8.91 days; 1970, 3.29 days. In order to test whether these differences were due entirely to differing proportions of juveniles, times were calculated taking into account the proportions of juveniles on the plots each year (Table 4); the meantimes of occupancy for the two age classes were assumed to remain constant (adults, 6.10 days; juveniles, 1.35 days). This allows mean times of occupancy of the plots as: 1967, 3.16 days; 1968, 3.16 days; 1969, 2.87 days; 1970, 2.68 days, so that annual differences in times spent on the plots were not entirely due to differences in the proportions of juveniles trapped. The higher rate of disappearance in juveniles could suggest that their mobility is greater than that of overwintered animals so that relatively more juveniles were captured.

If a large part of the home range was off the plots, occupancy of the portion being trapped would be low. Times of capture and the lengths between recaptures (Appendix II) suggest that home ranges may be much larger than the minimum ranges shown in Figure 8. The small decrease in mean times of occupancy with decreasing population levels could result from an increase in size of these home ranges such that even less time was spent on the portions included in the trapping area. The return of marked animals after long absences (Appendix II) also indicates that portions of the "lifetime range" (Jewell, 1966) of some individuals lie on the plots and occupancy time would be expected to be short in many cases and fleeting in others.

Autopsy

Body weights

Krebs (1964) used body weight in mid-summer as an indication of "cycles," with high body weights occurring only at population peaks. Mean body weights of all overwintered animals autopsied during the present study were calculated (Fig. 10 and Appendix III). Because there was no evidence of increasing weight due to fat deposition towards the ends of the collecting periods and because sample sizes are small, weights of all autopsied overwintered animals except those which had been maintained in captivity (Appendix IV) were used each year. Chipmunks were collected at various times of the year and in various vegetative associations with no apparent bias.

Mean weights of overwintered animals (sexes combined) declined from 1967 to 1969 with increases in 1970 and 1971 (Fig. 10). The difference was significant between 1967 and 1969 and close to significant

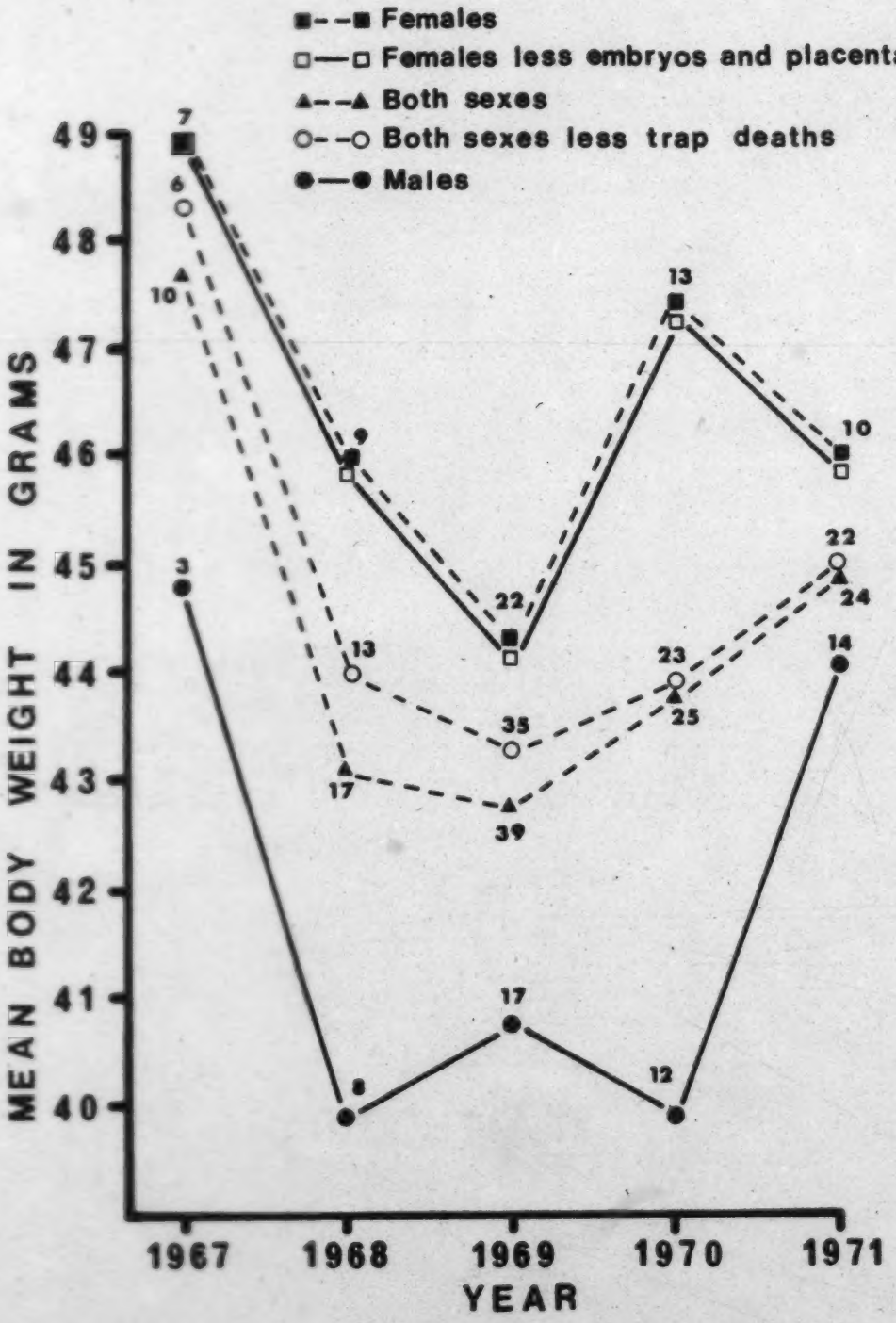


Figure 10. Changes in mean summer body weight of overwintered chipmunks throughout the study. Sample sizes are shown for each point.

Table 6. Comparison of mean body weights of overwintered animals compared throughout the study. N = sample size

a)

Year	Comparison	N	Student's "t"	Probability
1967	♂♂ vs ♀♀	10	0.998	N.S.
1968	♂♂ vs ♀♀	17	2.111	<0.10
1969	♂♂ vs ♀♀	39	1.871	<0.10
1970	♂♂ vs ♀♀	25	3.864	<0.01
1971	♂♂ vs ♀♀	24	0.689	N.S.

b)

Years compared	Total overwintered animals			Females			Males		
	"t"	N	P	"t"	N	P	"t"	N	P
1967 vs 1968	1.846	26	<0.10	0.918	15	N.S.	1.267	10	N.S.
1967 vs 1969	2.295	48	<0.05	1.668	28	N.S.	1.127	19	N.S.
1967 vs 1970	1.733	34	<0.10	0.553	19	N.S.	1.354	14	N.S.
1967 vs 1971	1.233	33	N.S.	0.849	16	N.S.	0.198	16	N.S.
1968 vs 1969	0.186	55	N.S.	0.601	30	N.S.	0.428	24	N.S.
1968 vs 1970	0.336	41	N.S.	0.507	21	N.S.	0.010	19	N.S.
1968 vs 1971	0.869	40	N.S.	0.012	18	N.S.	1.935	21	<0.10
1969 vs 1970	0.640	63	N.S.	1.356	34	N.S.	0.577	28	N.S.
1969 vs 1971	1.303	62	N.S.	0.568	31	N.S.	2.114	30	<0.05
1970 vs 1971	0.624	48	N.S.	0.453	22	N.S.	2.537	25	<0.05

Table 7. Sex ratios in different age classes as determined by annuli on the diastema of the dentary for all autopsied animals, and breeding condition of females

B = breeding females; N = non-breeding females

Year	Age class															Total		%B (in over-wintered ♀♀)
	Juvenile		1			2			3			4						
	♂♂	♀♀	♂♂	♀♀ B	♀♀ N	♂♂	♀♀ B	♀♀ N	♂♂	♀♀ B	♀♀ N	♂♂	♀♀ B	♀♀ N		♂♂	♀♀	
1967	10	9	3	2	2	1	1	0	0	2	1	0	0	0		14	17	62.5
1968	15	9	7	2	4	4	4	0	0	1	0	0	0	0		26	20	63.6
1969	21	18	11	5	6	6	4	2	2	5	0	0	0	0		40	40	63.6
1970	21	20	10	3	0	2	3	2	0	2	0	1	3	0		34	33	84.6
1971*	8	3	10	3	3	2	2	0	1	3	0	0	0	0		21	14	72.7
Total	77	61	41	15	15	15	14	4	3	13	1	1	3	0		137	126	69.3
♀♀B	0			50			77.8			92.9			100			69.2		

*The skulls of four animals were lost and consequently could not be aged.

($0.05 < P < 0.10$) when 1967 and 1968 were compared and when 1967 was compared with 1970 (Table 6).

On average, females were heavier than males, although this was significant only in 1970 when the percentage of breeding females was higher than in previous years (Table 7). Sexes were separated (Fig. 10) in order to investigate whether changes in mean body weights occurred in both sexes. Few pregnant females were obtained in most years, and the proportion breeding was largely determined by the presence of placental scars. Mean body weights of all overwintered females in which the weights of placentae and embryos were subtracted from the weights of pregnant females did not vary appreciably from the mean figures without that subtraction so that pregnancies can not account for the annual changes. Similarly, no appreciable change was evident when chipmunks which had died in the live-traps and were generally lighter in weight were excluded from the total samples. There was no significant difference in body weights of females from year to year, while males showed a significant weight increase in the last year.

Breeding season

Copulation occurs soon after chipmunks emerge from hibernation (Criddle, 1943; Forbes, 1966a; Sheppard, 1969; Broadbooks, 1970a), and was observed only once during the course of this study--on 26 April, 1969. Reimers' (1960) suggestion that copulation occurs in *E. sibiricus* before the females leave their burrows was disproved by Shtil'mark (1963).

Births occur at the end of May or in early June (Forbes, 1966a) after a gestation period of approximately 30 days (Criddle, 1943; Clothier, 1969). Three pregnant females gave birth in captivity at

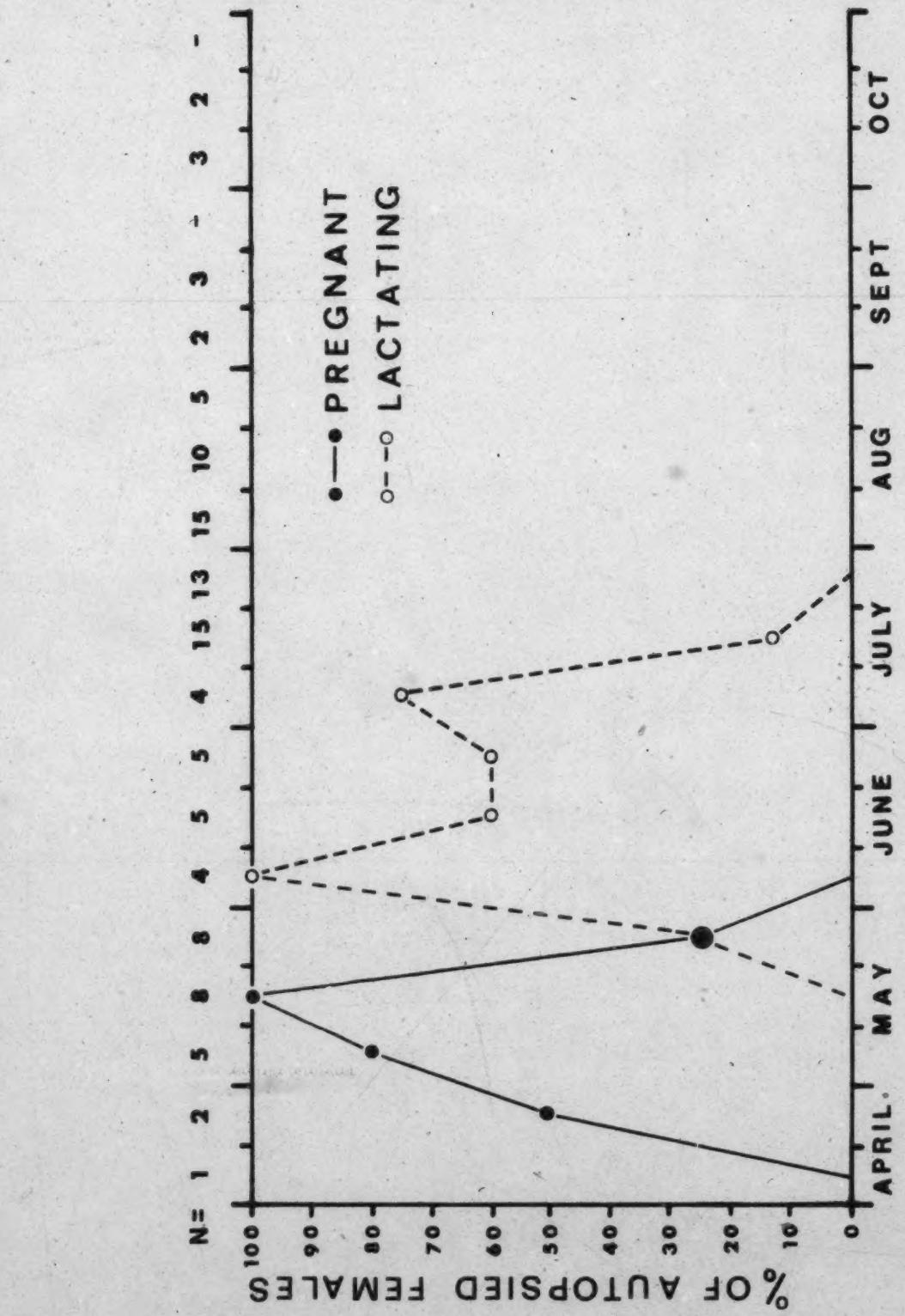


Figure 11. Percentages of pregnant and lactating females in autopsied sample. N shows the sample size for each 10-day period.

Heart Lake on May 29, June 5 and June 8, 1967. No pregnancies were recorded after the end of May, and lactation, revealed by the expression of milk from nipples, was not observed after the end of July (Fig. 11). Juveniles were first observed, either in live-trapping or in the autopsied sample, on: July 20, 1967; July 19, 1968; July 18, 1969; July 11, 1970 and July 18, 1971.

Age determination

Insufficient autopsies were performed on animals of known age to be certain that a single annulus of denser bone on the diastema of the dentary actually corresponded to one year's growth, but the few animals in that category supported this assumption. Using this technique, the individuals autopsied were assigned to age groups (Table 7).

No temporal pattern was common to the autopsied samples each year. For instance, in 1969, 33 chipmunks (41 percent of the total sample for that year) were collected before the appearance of the first juvenile, while in 1970 only 14 (19 percent) were collected before that time. Because all animals were incorporated into the samples, the ratios of animals older than one year should be comparable provided that there are no age-specific differences in mortality among those individuals during the collecting period. Live-trapping on the plots was of consistent intensity between years, so that the proportion of juveniles in those samples is comparable. The proportion of live-trapped juveniles, determined on the basis of body weight (Table 4), can now be incorporated into a yearly model showing population composition (Fig. 12).

The proportions of the total population found in various age classes varied somewhat from year to year (Fig. 12). Any differences

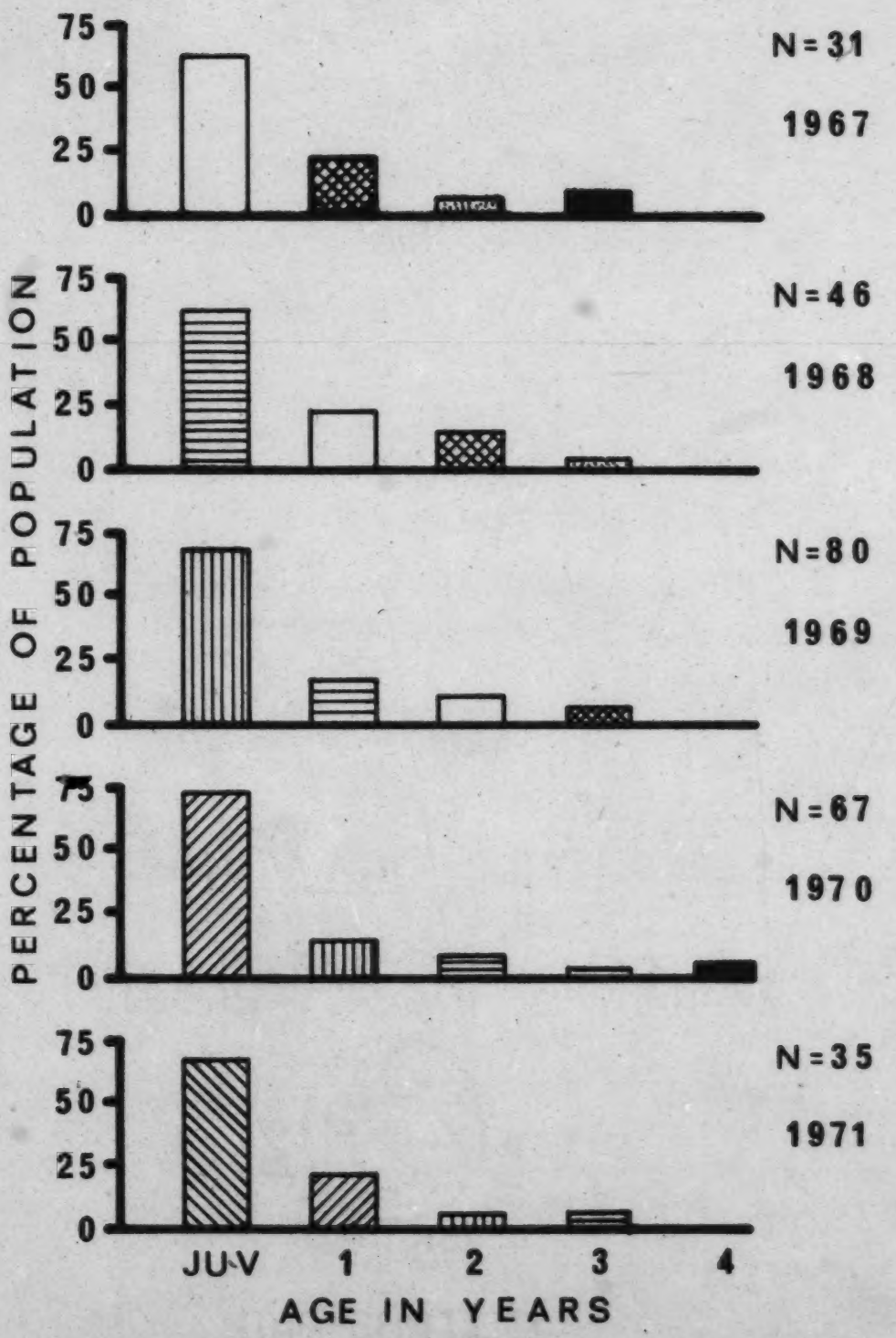


Figure 12. Model showing percentage of population found in each age group each year, calculated from live-trapped juveniles and autopsied overwintered animals.

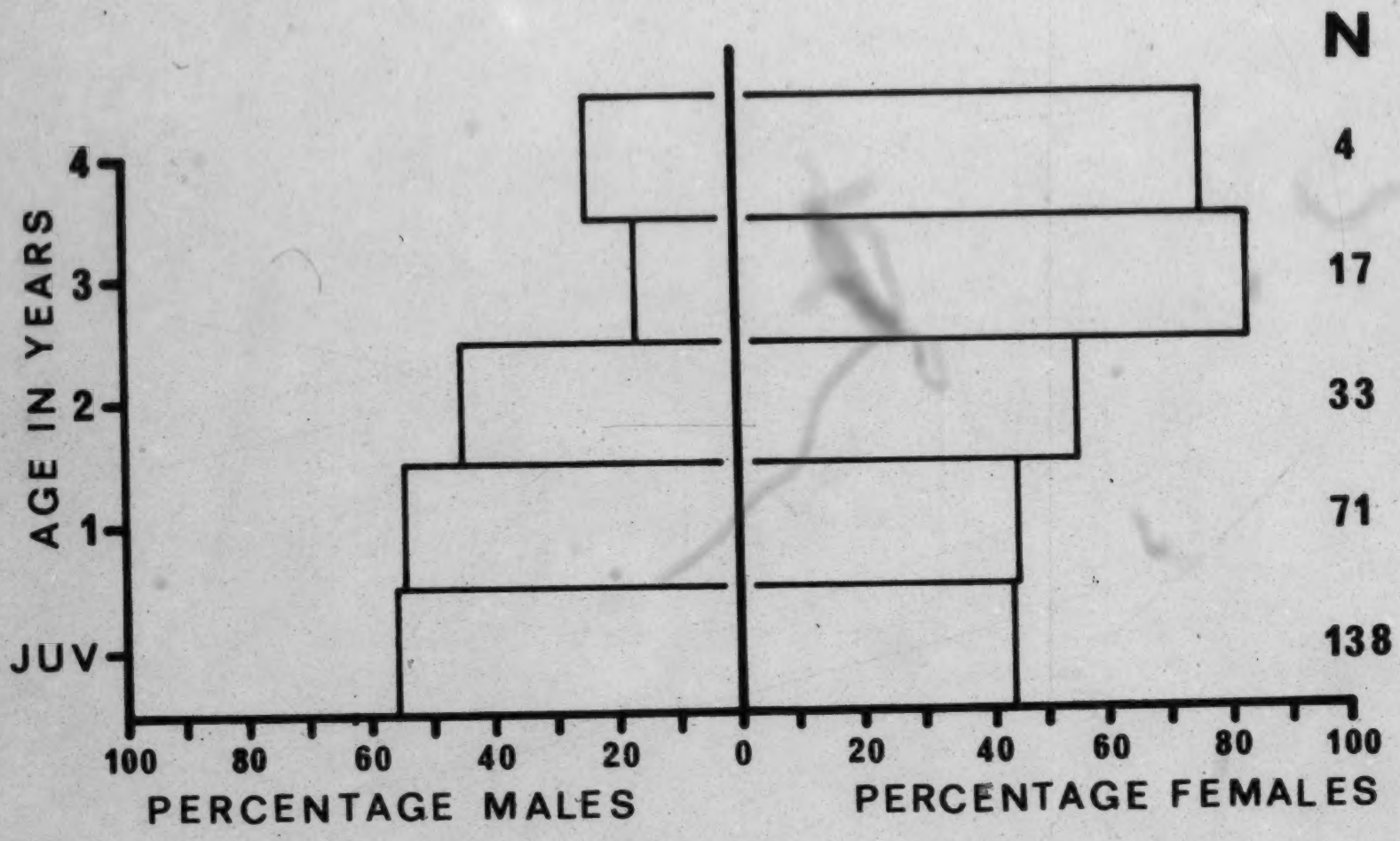


Figure 13. Change in sex ratio with age. N = sample size.

in the proportions of age classes may affect potential recruitment in the population. Except for the strong cohort which was born in 1966 and was the only one to reach four years of age, annual differences in population structure were small, although potential recruitment could still have been affected. That cohort born in 1964 also appeared to be slightly larger when three years old than three-year-old cohorts in other years, but may be a biased result because of the small numbers involved.

Sex ratio

No difference from parity was observed in the sex ratio of autopsied animals for each year (Table 7), so that the apparent difference on the plots in 1968 (Table 3) was possibly a consequence of smaller numbers and a trapping bias favoring males. With their probably larger home ranges, males would be trapped as occasional visitors on the plots from distances further than females.

The percentage of females increases with age (Fig. 13), and although this change in sex ratio is not statistically significant, the trend is there and a change in age structure of the population could result in a change in the sex ratio. A sex ratio biased toward males should result from any increase in the proportion of younger age classes in the population while the ratio would be biased toward females if older age classes predominated.

However, the increase in males live-trapped on the plots in 1968 does not appear to result from a decrease in the average age of the population. In that year the proportion of males was high (66%) while the percentage of juveniles was relatively low (62%). It was not

possible to determine the proportion of yearlings in live-traps, but combined juvenile and yearling age classes in the autopsied samples comprised: 1967, 84.2%; 1968, 84.5%; 1969, 86.0%; 1970, 84.0%; 1971, 87.0%.

Percentage breeding

Sheppard (1969) stated that "in western Alberta approximately one third of the yearling chipmunks do not breed." Sexually mature females were distinguished throughout summer by the presence of embryos before parturition or placental scars after the breeding season. Placental scars remained obvious until at least the end of the collecting period, and autopsies on animals held captive over winter showed that scars could still be distinguished in February. Breeding and non-breeding males could not be distinguished from one another.

Near Heart Lake fifty percent of the yearling females bred compared with 39.6% in *E. minimus* in Sheppard's (1969) investigation (Table 7). The proportion increased with age, so that all four-year-old females at Heart Lake bred. This increase suggests that the more "settled" or experienced females participate in breeding while younger females are possibly still seeking areas of non-harassment or areas with a better food supply.

Participation in reproduction by females was greater in 1970 and 1971 than in previous years (Table 7). The slightly increased population on the plots in 1971 may be, in part, a reflection of the increased percentage of breeding females in 1970. Although the sample size is small (N = 3), the increase in breeding by yearling females may be an important factor. Some correlation with population density is evident in the present study in that breeding (in the autopsied sample) was highest when gross density (in the live-trapped sample) was low, although

it did not increase with declining population from 1967-69.

The proportion of overwintered females breeding did not change to any extent when populations on the plots exceeded approximately 24 animals (Fig. 14), while below that number breeding increased with a reduction in population size. The "critical density," above which the percentage of overwintered females breeding did not seem to be influenced by increasing density, was thus approximately 0.35 chipmunks per hectare (0.8/acre). This density allows a mean occupancy area of 0.5 hectares per chipmunk (1.3 acres/chipmunk) which is in reasonable accord with the adult female minimum home range calculated in this study (0.3 hectares). Unfortunately, actual numbers of breeding females on the plots each year could not be ascertained because no external signs of breeding were visible once lactation ceased.

Although testis weight does not necessarily reflect breeding ability in sciurids (Hoffman and Kirkpatrick, 1956), changes in testis size and weight do occur with season in chipmunks. A definite relationship exists between the weight of a single testis (after fixation) and the "testis coefficient" (length in mm x width in mm), so that changes in the testis coefficient throughout summer indicate changes in testicular development (Fig. 15). Sperm were found in the seminiferous tubules of all testes with a coefficient above 45, but in no testes with a coefficient below that value.

Even in the breeding season a number of males, including some three-year-olds did not have testis coefficients even close to 45 (Fig. 16) and it would appear that those animals did not attain sexual maturity. The latest date on which sperm were found in seminiferous tubules was May 22

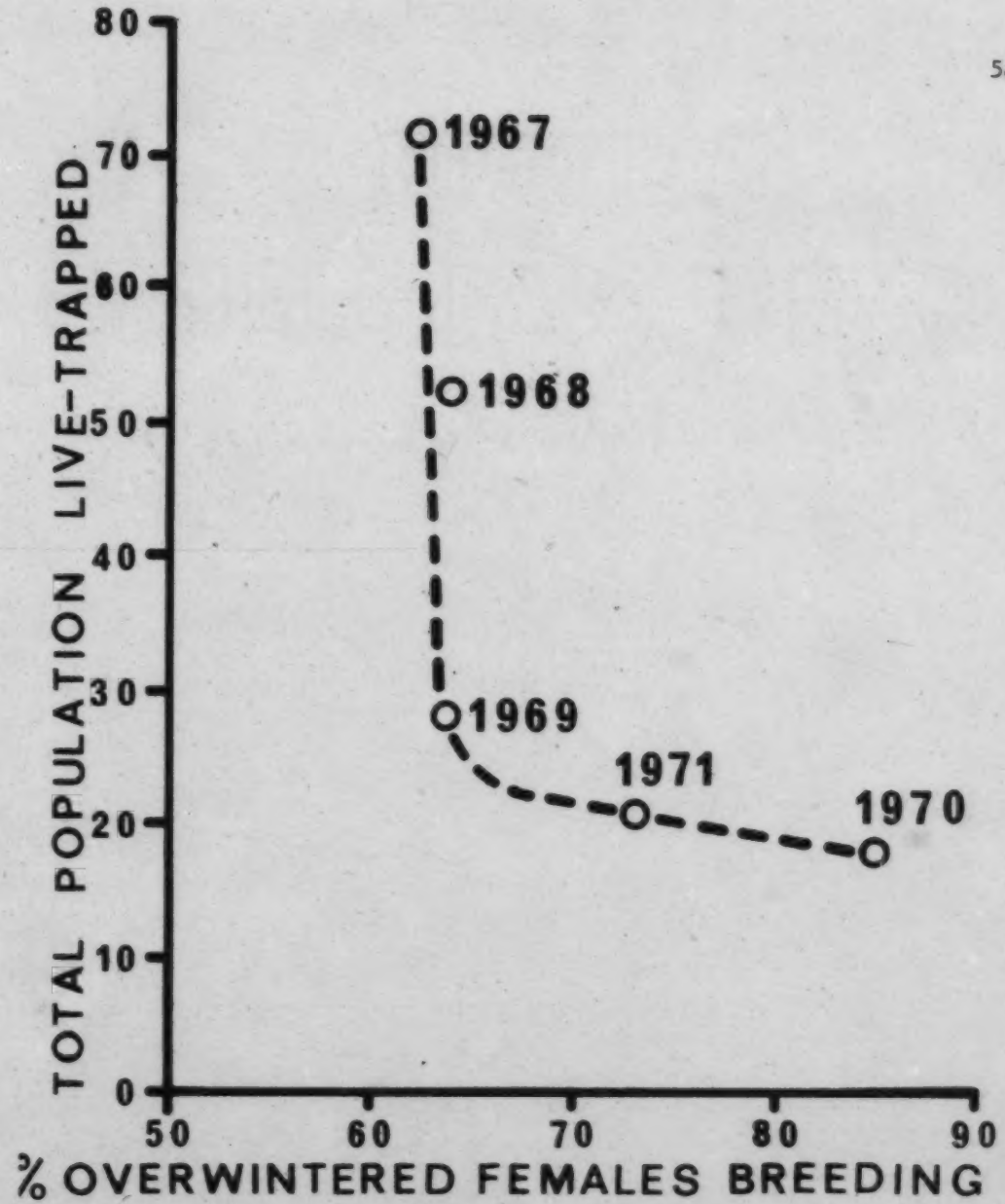


Figure 14. Percentage of overwintered females breeding (autopsied sample) at different population levels (live-trapped sample).

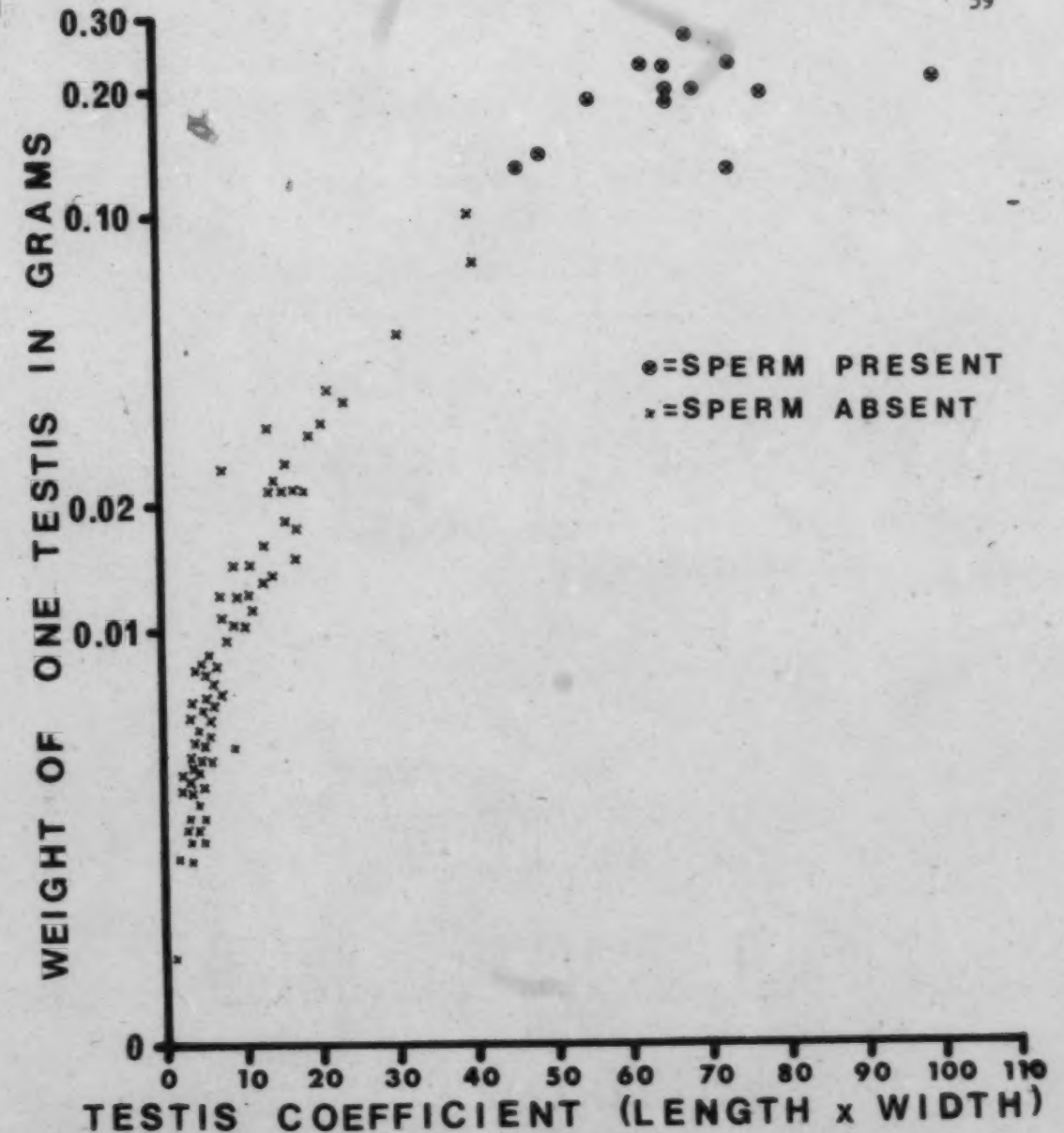


Figure 15. Relationship between weight of a single testis and testis coefficient.

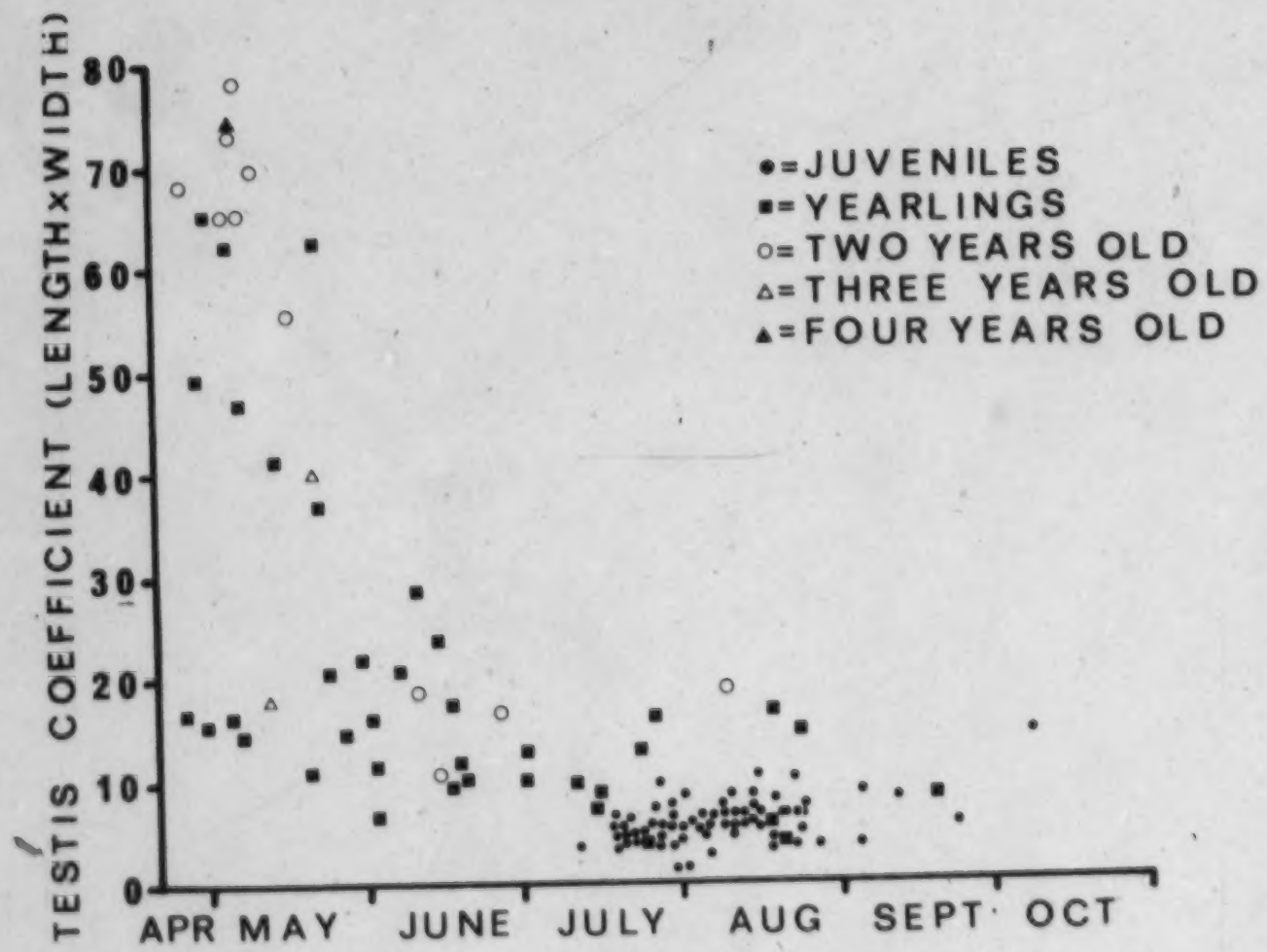


Figure 16. Seasonal changes in testis measurements (all years pooled). All testes with coefficients above 45 contained sperm.

and some males with enlarged testes did not have sperm present prior to that date, indicating either no potential for breeding or an earlier involution of testes in potentially reproductive animals. The lack of sperm after the end of May also confirms a single annual breeding season.

Males one year of age or older generally had testes larger than those of juveniles from July to the end of the collecting period. Older males may have shown involution from either the group with enlarged testes and the presence of sperm in spring or from the group with smaller testes and no sperm at that time. An evaluation of the percentage of males which definitely reached breeding potential is not possible because there is no evidence that males with larger testes in, say, August had previously bred while those with smaller testes had not, although such may well be the case. Not all males attained full reproductive status and most non-breeding males, as evaluated from spring results, appeared to be yearlings so that the proportion of breeding males may increase with age as occurred in females.

Forbes (1966b) found significant differences between "adults, subadults and juveniles" in the means of orbitonasal length (ONL) and interorbital breadth (IOB). Chronologically, his maximal ages for those relative age classes were: juvenile, to 100 days; subadults, 60 to 90-100 days; adults, over 100 days. As his "subadults" were non-overwintered animals, they have been included in the juvenile cohort in the present study. Since no breeding occurs during the first summer of life, it appears feasible to classify those animals as juveniles rather than subadults even though adult body measurements are approached. There are differences in total length (TL) and zygomatic breadth (ZB) as well as ONL and IOB between age classes in the present study (Appendix V and Table 8).

Table 8. Comparison between means of various measurements for different age classes and reproductive criteria. TL = total length; ZB = zygomatic breadth; ONL = orbitonasal length; IOB = interorbital breadth; B = breeding; NB = non-breeding

Age classes compared	Value of "t"			
	TL	ZB	ONL	IOB
3 vs 2 (both sexes)	0.0360	1.4915	0.0376	0.4836
2 vs 1 (both sexes)	1.1500	2.9546***	1.8578*	2.3965**
1 vs juv. (both sexes)	6.2041****	7.8793****	7.3692****	4.1627****
1 (B) vs 1 (NB) (females)	2.3213**	1.6937	2.4117**	1.7832
1 (B) vs 2 (females)	0.6381	0.6661	0.3485	1.0532
1 (NB) vs 2 (females)	1.7985	3.2041***	2.1595**	3.5968***

****P < 0.001; ***P < 0.01; **P < 0.05; *P < 0.10.

Four-year-olds were not tested because of the small sample size (N = 4), but no differences were found between measurements for animals in age classes two and three. Two of the four measurements reveal differences between yearlings and two-year-olds, suggesting some variation within the yearling group. Highly significant differences, as would be expected, existed between yearlings (included in Forbes' "adults") and juveniles (Forbes' "juveniles" plus "subadults").

The proportion of females showing signs of breeding is considerably smaller (50%) among yearlings than in older age groups (83%). This suggests that variation among yearlings may be reflected in the breeding status of the individuals concerned. Breeding yearling females had significantly larger means than non-breeders in two of the four cranial measurements (Table 8). Forbes (1966b) found significant sexual dimorphism in cranial measurements and, as males could not be distinguished as breeders or non-breeders in the present study, attention was focused on females. In females no difference in cranial measurements was found between breeding yearlings and two-year-olds, but significant differences existed between non-breeding yearlings and two-year-olds, suggesting that adequate somatic development was necessary for reproduction to occur.

Differences in cranial measurements (Table 8), signifying a greater size in breeding yearlings, were borne out by an analysis of mean body weights of autopsied animals (Table 9). Weights of embryos and placentae were subtracted from total body weights in order that the results should not be biased. Again, it appears that only those yearlings which had attained a size not different from two-year-olds were able to breed, while smaller yearlings did not participate in reproduction.

Table 9. Comparisons between mean body weights of autopsied females in various age classes. Weights of embryos and placentae have been subtracted from the total weights of pregnant animals.

B = breeding; NB = non-breeding; N = number in sample

Age	Reproductive condition	Mean weight in grams	N
1	B + NB	43.43	28
1	NB	38.45	13
1	B	47.74	15
2	B + NB	47.12	18
3	B + NB	46.32	14

Age classes compared	"t"	Significance
1 (B + NB) vs 2 (B + NB)	1.54	N.S.
2 (B + NB) vs 3 (B + NB)	0.32	N.S.
1 (B) vs 1 (NB)	5.81	$P < 0.05$
1 (NB) vs 2 (B + NB)	3.52	$P < 0.05$
1 (B) vs 2 (B + NB)	0.27	N.S.

Embryonic contribution

Differences in recruitment each year may be influenced by both the number of embryos successfully brought to term and contributed to the population (Table 10) and by survival during weaning. Resorption of some embryos was evident during the period of gestation (Table 11), and those losses are not included in the estimation of embryonic contribution. Shtil'mark's (1967) postulate that reproductive contributions decline when population density increases was not borne out as there was no relationship between populations on the plots and the embryonic contribution each year.

However, the effective embryonic contribution was affected by the proportion of females in each age class which actually bred. Table 10 also shows the embryonic contribution from breeding females, and the difference between contributions from total females and breeding females shows the differences which arose in the contribution of new-born young each year. The number of embryos contributed by breeding females did not vary significantly either from year to year or with increasing age, so that females which did breed seemed to reach their maximum potential at all times.

Prenatal mortality occurred each year (Table 11). Preimplantation losses (failure of ova to implant) were slightly higher than post-implantation losses (resorption of embryos). At least at the population levels encountered in the present study, no density-dependent mechanism appeared to function at the prenatal level, although losses were least in 1971. This again suggests that females which did breed were not unduly affected by their external surroundings once copulation had occurred or

Table 10. Embryonic contribution from total overwintered and breeding females from various age classes during the study. E = number of embryos; T = total females in age class; B = breeding females in class

Year	Age class 1			2			3			4			Total E	E/T	E/B
	T	B	E	T	B	E	T	B	E	T	B	E			
1967	4	2	10	1	1	5	3	2	10	0	0	0	25	3.13	5.00
1968	6	2	8	4	4	17	1	1	6	0	0	0	31	2.82	4.43
1969	11	5	21	6	4	18	5	5	22	0	0	0	61	2.77	4.36
1970	3	3	14	5	3	15	2	2	9	3	3	13	51	3.92	4.64
1971	6	3	14	2	2	11	3	3	9	0	0	0	34	3.09	4.25
Total	30	15	67	18	14	66	14	13	56	3	3	13	202	3.11	4.49
E/T	2.23			3.67			4.00			4.33					
E/B	4.47			4.71			4.31			4.33					

Table 11. Ovulation rate and prenatal loss in breeding females, determined by counting the numbers of corpora lutea and the numbers of embryos

Year	N	Corpora lutea	Ovulation rate	Pre-implantation loss	Post-implantation loss	Twinning	Total prenatal loss (%)
1967	6	32	5.33	1	1	0	6.25
1968	6	32	5.33	1	2	0	9.38
1969	15	70	4.67	4	1	1	5.71
1970	11	56	5.09	1	2	0	5.36
1971	9	44	4.89	1	0	0	2.30

that they were normally located in favored places.

Mortality

If the number of overwintered females captured on the plots each year (Table 4) is multiplied by the percentage of overwintered breeding females from the shot samples (Table 7), an estimate of the number of breeding females on the plots can be calculated. Provided that the annual effective embryonic contribution per breeding female in the shot samples (Table 10) holds for the plots as well, as seems likely, and that there is no postnatal mortality prior to capture of the juveniles, estimates can be made of the numbers of juveniles that should have been captured (Table 12).

Actual numbers of juveniles trapped on the plots were not significantly different from those calculated in three of the five years and more were captured than expected in the other two years. More juveniles were usually captured than expected, possibly because of their large home ranges in that some may have been captured after being born off the plots. The assumption of no mortality during weaning was supported by the fact that calculated numbers of juveniles were always near or less than the real numbers. The large excess trapped in 1968 and 1969 may have been a reflection of greater juvenile mobility toward the end of summer as more juveniles were trapped after mid-August in those years than in other years and the trapping period was longer (Fig. 6).

Longevities of up to six years in *E. minimus borealis* (Criddle, 1943), seven years in *E. townsendii* (Gashwiler, 1965) and eight years in *E. quadrimaculatus* (Ross, 1930) have been reported, although the oldest inhabitants in this study were only four years old. The cohort born in

Table 12. Actual and theoretical numbers of juveniles and total populations on the plots

Year	Theoretical number of juveniles	Real number of juveniles	P*	Theoretical population	Real population
1967	17 x .625 x 5.00 = 53.12	44	N.S.	80.12	71
1968	8 x .636 x 4.43 = 22.54	33	<0.01	44.54	53
1969	4 x .636 x 4.36 = 11.09	19	<0.001	20.09	28
1970	3 x .846 x 4.64 = 11.78	13	N.S.	16.77	18
1971	4 x .727 x 4.49 = 13.06	14	N.S.	20.06	21

P* = Theoretical and real juvenile numbers compared by X^2 test.

1966 comprised a rather larger proportion of the population in the years after overwintering than did cohorts born in 1967, 1968 and 1969 (Fig. 12). Those born in 1966 were also the only ones during the course of the study to reach four years of age. The cohort born in 1970 also seemed to be larger than those of the previous three years.

To calculate age-specific mortality, the percentage of the total population in a particular age class was divided by the percentage of animals in the preceding age class the previous year (Table 13). Average survival between years remained fairly constant, although it seemed to be lower between 1968 and 1969 and higher between 1970 and 1971. Survival from juvenile to yearling was generally lower than that of yearlings to two-year-olds or two-year-olds to three-year-olds. The very low average survival (0.199) from three to four years of age resulted from the fact that animals of that age were found only in 1970.

Provided that there was no summer mortality during the collecting periods, the average probability of a juvenile reaching two years of age is a factor of the survival rates for both between-collecting periods (i.e. 0.288 x 0.467 = 0.135), while the probability of its reaching three years of age is reduced even more (P = 0.288 x 0.467 x 0.407 = 0.055). This means that only about five of every 100 animals weaned reached three years of age. To judge from the average survival rates between age groups, very few four-year-olds would be expected (P = 0.011, or about one hundredth of those weaned). The possibility exists that the cohort born in 1966 was larger than usual or, if not, at least had an increased survival rate. Its survival rate from 1967 to 1968 was certainly greater than for other cohorts of that age in other years.

Table 13. Age-specific survival rates throughout the study

Years	Age increase				Yearly average
	J---→1	1---→2	2---→3	3---→4	
1967-68	0.36	0.62	0.27	0	0.42
1968-69	0.28	0.42	0.39	0	0.36
1969-70	0.21	0.44	0.23	0.80	0.42
1970-71	0.31	0.39	0.73	0	0.48
Average	0.29	0.47	0.41	0.20	

If the number of immigrants is equivalent to the number of emigrants, a decline in the proportion of juveniles trapped between mid-July and the end of the collecting season (usually the end of August) would represent mortality in those juveniles. The percentage of juveniles in five-day periods following their first appearance (either in the live-trapped or shot sample) is shown in Figure 17. In both live-trapped and autopsied animals there was no general decrease in the proportion of juveniles collected with time, suggesting that mortality was probably not an important factor in that age group during the collecting period. Immigration to fill a void is unlikely for the whole population (as sampled in the autopsies), so that, in this case, mortality was investigated.

The low percentage of juveniles on day 45 may indicate mortality, although that time was normally outside the collecting periods. The large numbers of juveniles trapped from days 50-55 again suggest increased mobility of that age class in fall, although live-trapping results were too few to demonstrate any plateau in population size with a sudden influx of immigrant juveniles in September.

Mortality rates were, however, higher for the juvenile cohort (Table 13). As it did not occur in the first six weeks or so of independent life, mortality must have occurred either in late fall if suitable food and overwintering sites were not established, during hibernation, or in early spring.

Although there appeared to be no mortality during most of the collecting periods, it seemed reasonable to expect a higher mortality among juveniles immediately upon their becoming independent, especially if maternal care ceased abruptly. Juveniles live-trapped and released

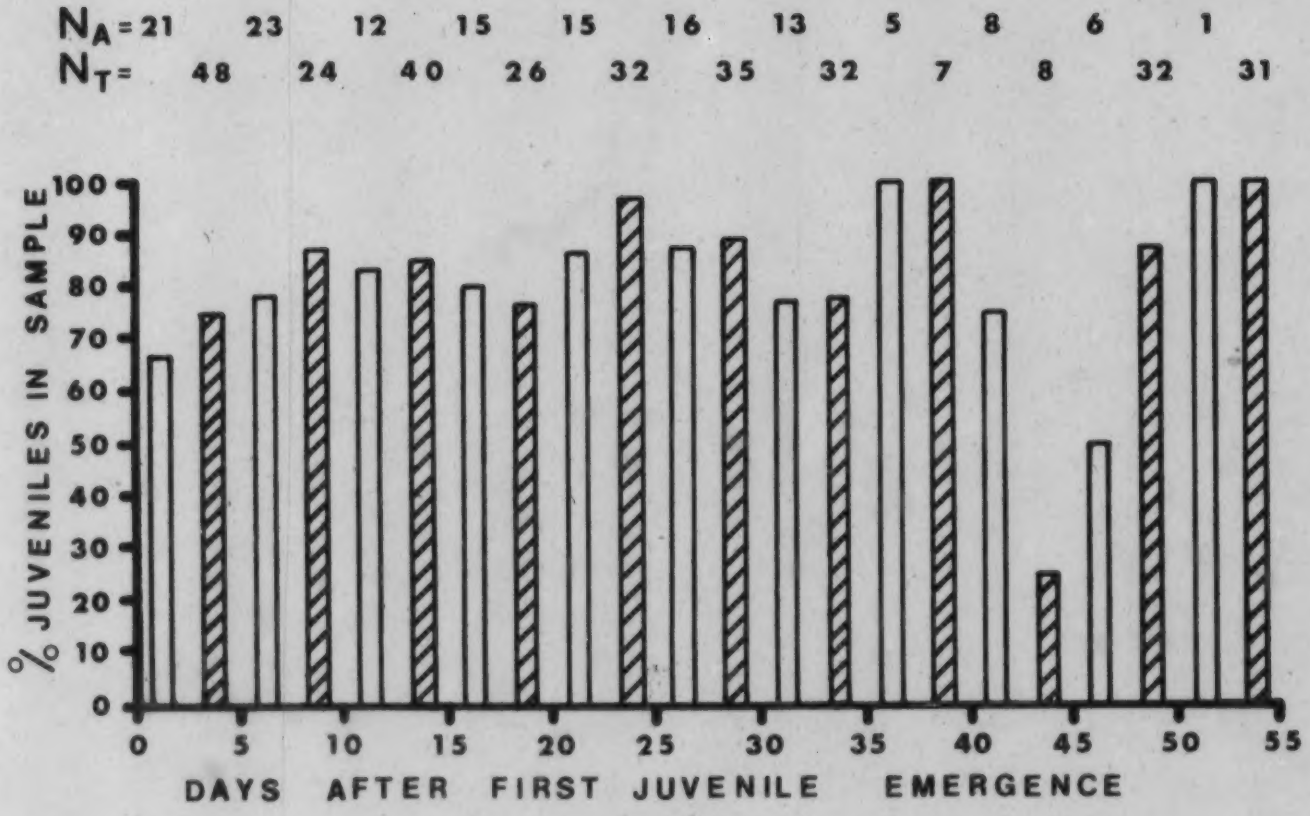


Figure 17. Changes in the proportion of juveniles in live-trapped (hatched) and autopsied (clear) samples following emergence. N_A is the autopsied sample size and N_T is sample size of live-trapped animals over periods of five days.

immediately upon their first emergence (in mid-July) did not return to maternal burrows. Several marked juveniles were followed for varying periods of up to 14 hours in 1968, but all remained above ground, obtaining shelter for the night wherever possible, usually crouching beneath rock overhangs or the roots of trees. It is probable that the presence of the observer was responsible for the unwillingness of juveniles to return to the maternal burrows because ranges of juveniles, females at least, seemed to follow the broad outlines of those belonging to adult females (Fig. 8).

Predation, which would be expected to be greatest at the time when juveniles first emerged, was probably light. A pair of great horned owls *Bubo virginianus* nested on Plot A in 1968 and 1969, but no pellets were found near the nest. However, feeding may have occurred elsewhere. Chipmunks also seemed to play a minimum role in the nutrition of ermine *Mustela erminea richardsonii* (D. Wooley, pers. comm.).

Winter Strategy

Burrows

Five burrows were excavated during the study and all were of the "simple" type (Criddle, 1943) with a single entrance leading via a tunnel approximately 1 meter in length to a terminal chamber measuring approximately 25 cm x 25 cm x 10 cm. No two-chambered burrows such as Allen (1938) and Panuska and Wade (1956) found for *T. striatus* and Snigirevskaya (1962) found for *E. sibiricus* were ever located.

The floor of the chamber in each burrow was covered by up to 15 cm of rotting leaves (usually *Alnus*), feces and twigs bound together with

fungus. The fungus usually extended over all the walls of the tunnel and chamber. These "fungus gardens" have been suggested as additional food reserves (Howell, 1929), and Tevis (1955) has shown that *Eutamias* eats fungus. They could also provide an additional source of heat from the fermentation process. None of the burrows contained food reserves when excavated.

All four animals in artificial hibernacula near Heart Lake in winter 1969-70 died in January. Hibernation had not occurred in any of the animals before their deaths, possibly from lack of adequate food supplies.

Microclimate temperatures inside one sand-based burrow were lower than those in one of four limestone-based burrows monitored during winter 1969-70 (Fig. 18). Temperatures in all burrows in limestone were similar, but that shown was the only one for which there is a complete record. The sand-based burrow was excavated on May 10, 1970 and found to be empty of supplies and, apparently, abandoned. The thermistor was at the entrance of the terminal chamber in this burrow, but the other burrows could not be excavated.

Although temperature differences in the burrows were far less pronounced, they followed roughly the fluctuations in air temperature until the heimal threshold was reached (Fig. 18). During excavation no blocking was observed in any of the tunnels, and neither Criddle (1943) nor Broadbooks (1958) found that any attempt had been made to seal the hibernaculum from direct communication with the soil surface. Once the heimal threshold was exceeded there was a slight temperature increase in the burrows and then relative stability during the coldest months.

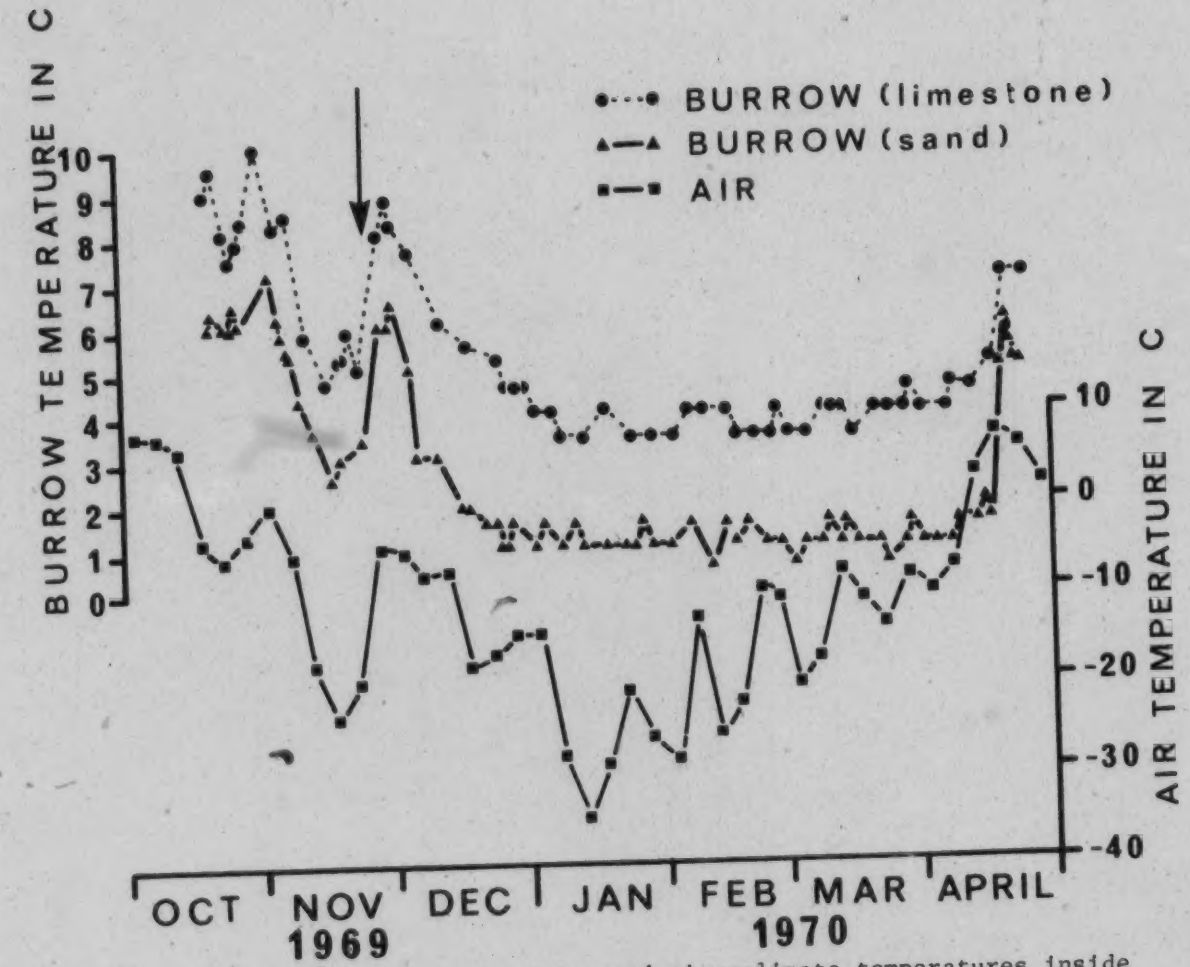


Figure 18. Mean air temperature and microclimate temperatures inside chipmunk burrows during winter 1969-70. The heimal threshold was exceeded at the point shown by the arrow.

Energy requirements

Oxygen consumption in one non-hibernating female chipmunk (weight: 42.8 g) at an ambient temperature of 2.5 C was continually monitored for 47 days from 13 January to 28 February, 1972. Several mechanical breakdowns and structural alterations caused the loss of six days' data, but the energy used during 41 days was calculated (Fig. 19). Daily energy requirements varied from 19.7 to 35.3 kilocalories with a mean of 27.0 kilocalories.

The resting metabolic rate (RMR) of that animal at 2.5 C was 5.7 cc O_2/g/hour. At thermoneutrality (30 C) a theoretical basal metabolic rate (BMR) may be calculated from the equation:

$$BMR = 3.8\ W^{-0.27}\ \text{cc } O_2/g/hr$$

where W is the weight in grams (Morrison *et al.*, 1959; as in Wang and Hudson, 1971). This allows a value of 1.4 cc O_2/g/hour. The thermal conductance, a measure of heat loss, can be calculated from the equation:

$$C = 1.01\ W^{-0.505}$$

(Herreid and Kessel, 1967; as in Wang and Hudson, 1971), and provides a value of 0.2 cc/g/hour/C. The slope of a regression line equivalent to the thermal conductance passes through the BMR at thermoneutrality (1.4 cc O_2/g/hour) and allows the theoretical RMR at 2.5 C to be calculated. The theoretical RMR at 2.5 C (5.6 cc O_2/g/hour) is very close to the observed value (5.7 cc O_2/g/hour), indicating that there was no evidence of torpor in that individual at low ambient temperature.

Thus, unless it hibernates, a normothermic chipmunk must maintain a RMR of approximately 5.7 cc O_2/g/hour throughout the winter. At 27.0 kilocalories per day throughout the hibernation period from mid-October to mid-April (180 days), approximately 4,850 kilocalories would

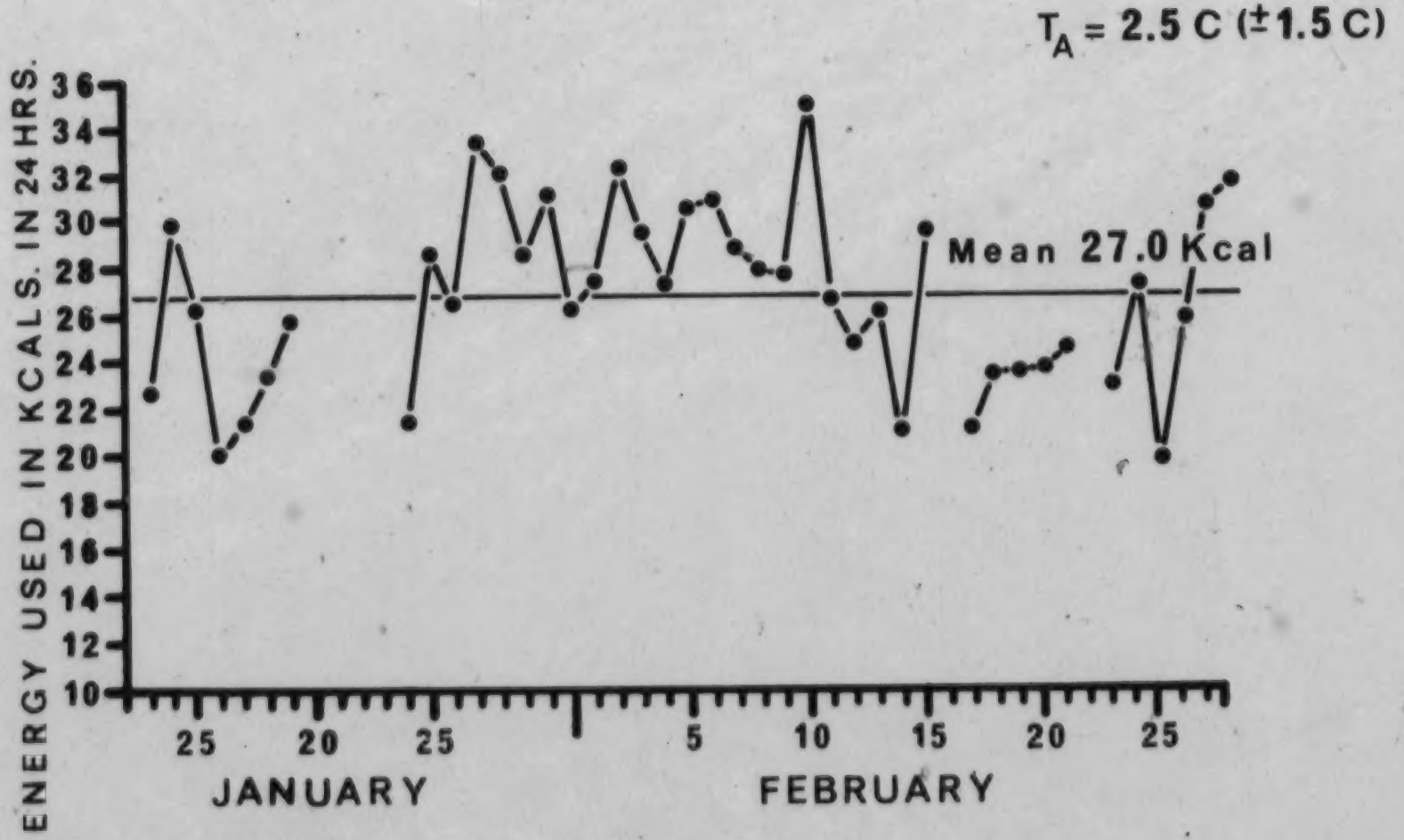


Figure 19. Fnergy used (in kilocalories) during 24 hours by a non-hibernating chipmunk (♀ P), weight: 42.8 grams) at 2.5 C. The mean requirement was 26.97 kilocalories per day.

be required to maintain a normothermic chipmunk at an ambient temperature of 2.5 C (variation: 1.8 C - 4.0 C).

Oxygen consumption was also measured in three hibernating chipmunks at ambient temperatures approximating those in the burrows, and the energy used in daily periods at different ambient temperatures was calculated (Fig. 20). No valid regression line can be affixed to these values (Spearman's coefficient of rank correlation $R_s = -0.17$), so that differences in energy requirements at those low ambient temperatures are probably not significant for hibernating chipmunks. Differences in ambient temperature between limestone- and sand-based burrows probably do not affect the energy requirements in hibernating chipmunks. The scatter in energy values is probably caused by different body temperatures even at identical ambient temperatures. Body temperature could not be monitored in the field, but the values obtained in the laboratory are shown (Fig. 20).

A mean value of 0.35 kilocalories per day was required by hibernating chipmunks at ambient temperatures similar to those in the burrows. The energy required for hibernation from mid-October to mid-April (180 days) using this mean daily requirement is 73.52 kilocalories so that hibernation, excluding any periods of arousal, is 76.4 times less costly than active life at 2.5 C for 180 days.

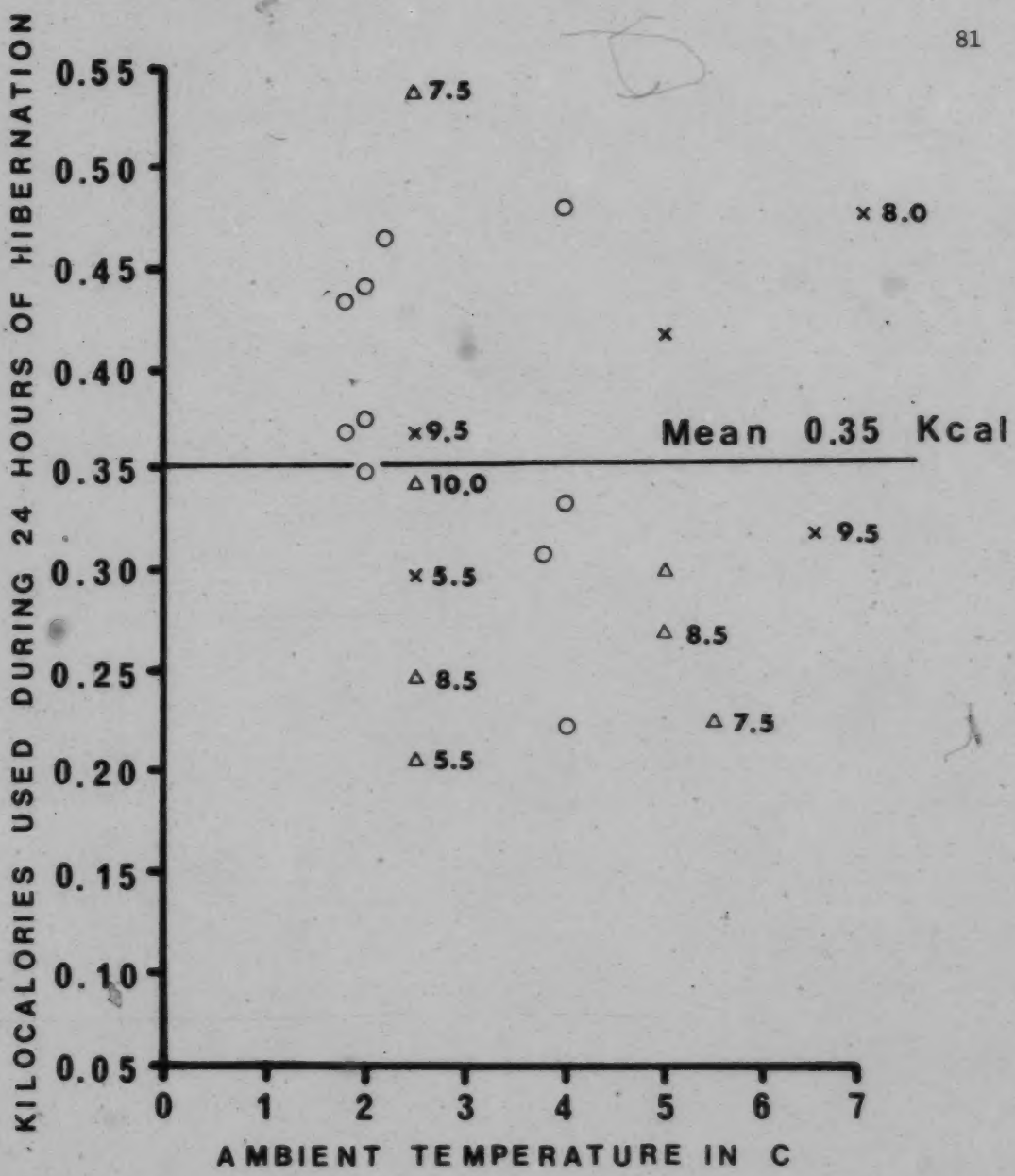
Of 18 chipmunks placed in a 5 C coldroom during winter 1971-72, only two hibernated--one on 7 October, 1971 and the other on [illegible] February, 1972. Daily examination of an undisturbed chipmunk (male E) allowed periods of arousal to be determined (Fig. 21). Continuous oxygen analysis of the second animal to hibernate (female 161) allowed the energy used in hibernation, arousal and re-entry into hibernation to be examined. Several

Figure 20. Energy used (in kilocalories) during 24 hours of hibernation. Figures on the graph indicate rectal temperatures in C.

△ ♂ A weight: 41.0-42.8 grams

× ♂ B weight: 45.7-51.3 grams

○ ♀ 161 weight: 44.0-44.2 grams


KILOCALORIES USED DURING 24 HOURS OF HIBERNATION
0.55
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
1
2
3
4
5
6
7
AMBIENT TEMPERATURE IN C
Mean 0.35 Kcal
△7.5
×8.0
×9.5
△10.0
×9.5
×5.5
△8.5
△8.5
△7.5
△5.5

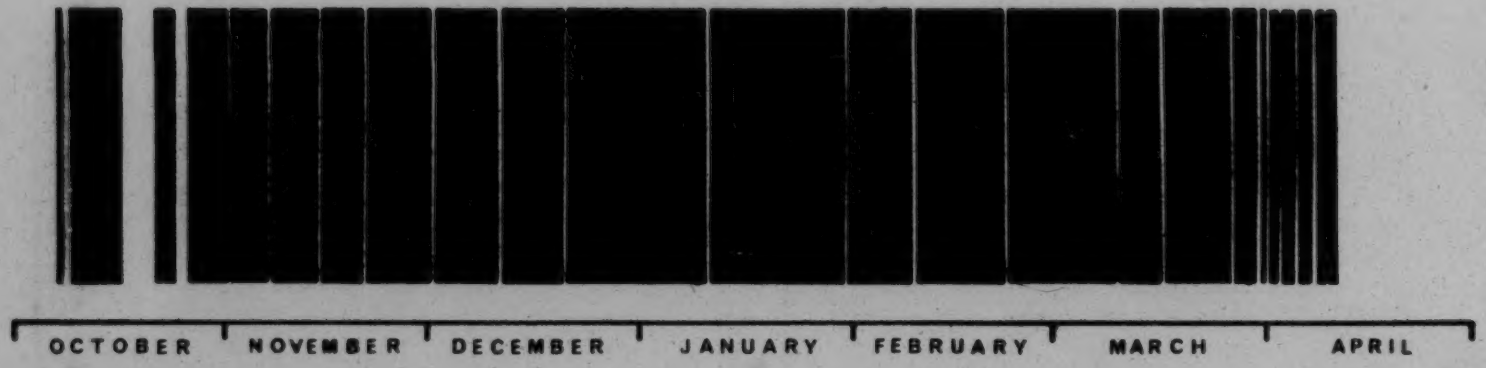


Figure 21. Periods of hibernation (dark areas) of one chipmunk (male E) in a 5 C coldroom during winter 1971-72.

of the measurements during hibernation have been incorporated into Figure 20.

Hibernation of male E began on 7 October, 1971 and continuous wakefulness began on 10 April, 1972, a period of 186 days. Arousal was more common near the beginning and end of this period (Fig. 21), with very short periods of arousal in mid-winter. One day of hibernation preceded arousal in October and April, and periods of hibernation reached a maximum of 21 days without arousal in December, 1971 and January, 1972. Food was consumed during each arousal period. As male E was not continually monitored, it was not possible to specify to hours the periods of wakefulness but continual monitoring of female 161 showed that, in four spontaneous arousals, approximately 12 hours were required for arousal and re-entry into hibernation. The arousal itself required 2 to 3 hours and no overshoot occurred in oxygen consumption. Similarly, re-entry into hibernation was smooth, following several small drops in energy requirements during the wakeful period. The time needed for re-entry into hibernation was also 2 to 4 hours.

Using these data, it was possible to estimate the energy required during the 186-day "hibernation period" in male E. Where arousal and re-entry into hibernation occurred on the same day it was assumed that 12 hours were spent at the level of wakefulness (energy required: 13.48 kilocalories) and 12 hours in hibernation (energy required: 0.18 kilocalories). Male E used 57.88 kilocalories during 164 days of hibernation and 593.30 kilocalories during 22 days of arousal and wakefulness, for a total of 651.18 kilocalories from 7 October, 1971 to 10 April, 1972, both dates inclusive. Had that male not hibernated

5,016 kilocalories would have been required so that, even with arousals, the conservation of energy during overwintering was 7.7 times more efficient in this hibernator with occasional spontaneous arousals than in a non-hibernating chipmunk.

Food

Winter

If the food stored for winter was insufficient to provide adequate energy for overwintering then winter mortality would ensue. An examination of hoarded food was considered advisable despite the fact that the possibility of its being limiting was considered remote by Broadbooks (1958; 1970a) and Cade (1963).

Several chipmunks with radioactive tags were followed to their apparent burrows in summer (July and August), 1970. Those burrows were excavated at the beginning of winter (12-14 October, 1970), but proved not to be winter burrows. None of the winter burrows in which microclimate temperatures were recorded were discovered until mid-September, so that it is quite possible that winter burrows were not established more than approximately one month before the beginning of hibernation. The energy available for overwintering, then, was not determined in this study.

Graves (1971) reported that, in *T. striatus*, individuals with low cache amounts did not hibernate. Feeding experiments were conducted at 5 C in the present study in order to determine whether the hoard itself or the availability of adequate food was a stimulus to hibernation (Table 14). All four chipmunks with restricted feeding (10 g of sunflower

Table 14. Effect of feeding regimens upon hibernation patterns. The experiment commenced 21 September 1971 and terminated 31 December 1971, after which all animals were allowed food *ad libitum* and were allowed to retain caches. All animals were at 5 C

Animal No.	Food	Cache	Date hibernated	Remarks
♂A	*ad lib.*	retained	-	
♂159	*ad lib.*	retained	-	
♂B	10 g/day	removed	-	Died 13.xii.71; no replacement
♂174	10 g/day	removed	-	Died 11.x.71; replaced by ♂165
♂C	10 g/day	added	-	Died 9.x.71; replaced by ♂F which died 26.xi.71
♂168	10 g/day	added	-	Died 10.x.71; replaced by ♂164
♂D	*ad lib.*	removed	-	Died 10.xi.71; replaced by ♂177
♂162	*ad lib.*	removed	-	
♂E	*ad lib.*	retained	7.x.71	Permanent arousal 10.iv.72
♀P	*ad lib.*	retained	-	
♂F	*ad lib.*	retained	-	Replaced ♂C in feeding experiment 9.x.71; died 26.xi.71
♀160	*ad lib.*	retained	-	
♀161	*ad lib.*	retained	14.ii.72	Permanent arousal 15.iii.72
♂164	*ad lib.*	retained	-	Replaced ♂168 in feeding experiment 11.x.71
♂165	*ad lib.*	retained	-	Replaced ♂174 in feeding experiment 12.x.71
♀166	*ad lib.*	retained	-	
♂169	*ad lib.*	retained	-	
♂177	*ad lib.*	retained	-	Replaced ♂D in feeding experiment 10.xi.71

seeds daily) had died by the end of December 1971, regardless of the addition or removal of a cache, and the experiment was terminated. Both males with food *ad libitum* and a retained cache survived, although one of two males with food *ad libitum* but a cache which was removed, died. Animals which replaced the original experimental animals experienced less time under experimental conditions, although this was inconsequential as hibernation did not occur in any of the animals in which food intake or cache availability was manipulated.

Seven chipmunks received food *ad libitum* and were allowed to retain their caches. Two of those animals hibernated - one for the entire winter (male E) and one for a short period in late winter (female 161). Two of four animals with food *ad libitum* and undisturbed caches in winter 1970-71 also died, while the remaining two hibernated for the whole winter.

The effect of food on hibernation could thus not be determined in the present study. Hibernation may possibly have been inhibited by noise or vibration in the coldrooms although, in most studies, some animals fail to exhibit hibernation (Scott and Fisher, 1972).

Summer

(i) Food available

Dyke (1971) showed that fruit production on the plants near Heart Lake was not constant from year to year, with berry production showing considerable variation. Fruit production was very good in summer 1966 so that overwintered berries were abundant in spring 1967. The cooler summer of 1967 was not conducive to heavy production, resulting in few overwintered berries in 1968. Fruiting was again poor in 1968, although strawberries and gooseberries *Ribes oxyacanthoides* produced better crops

than in 1967.

No measurements were made of fruit production in the years following Dyke's study, but 1969 seemed to be a poor year for all crops of berries. The warm summer of 1970, which was clearly the year of greatest variety in berries, produced a large crop of raspberries *Rubus strigosus* and bearberries as well as some relatively rare species such as black currant *Ribes hudsonianum* and red currant *Ribes triste*. Overwintered bearberries were common in spring 1971. Fruiting in raspberries and bearberries was poor in summer 1971, but berry production increased in bastard toadflax, bunchberry *Cornus canadensis*, high bush cranberry and, particularly, bog cranberry.

The population of chipmunks at Heart Lake is thus not restricted by the vagaries of crop production from a single species as Shtil'mark (1963; 1967) found in Western Sayan, USSR. However, a failure in crop production in one species was not always compensated by production in other species. The food available to *E. minimus* may not always be adequate for survival in all habitats. Years of poor seed production seem to correspond with the times of greatest population decline (1968 in particular).

(ii) Foods eaten

Stomach analyses from 262 chipmunks autopsied showed that 132 contained food while 130 were empty (either because feeding had not begun or because the animal died in a live-trap after previously emptying its stomach during confinement). Sixteen stomachs (6.1%) contained the spirurid nematode *Protospirura* (=*Mastophorus*) *muris*, a common stomach nematode in rodents. The infections were probably acquired by eating insects, some of which are known to be intermediate hosts (Chandler and

Read, 1930; Skriabin and Sobolev, 1963).

Most of the foods eaten were vegetable matter (Table 15). Arthropod parts comprised a moderately high frequency of occurrence (34% of those stomachs which contained food) but had a much lower percentage composition in individual stomachs (seldom more than 5%). Beetles, a grasshopper and a moth were identified, although mastication and partial digestion normally prevented identification. Mites and fleas were probably ingested during grooming. No vertebrate matter was found in the stomachs. Harriot (1940), Hesterburg (1950), Shackleford (1966) and Krull (1969) have all reported observations of *T. striatus* eating vertebrate matter, but *E. minimus* is not so omnivorous.

Because stomachs were not weighed, it was not possible to determine the percentage composition by weight of the various species eaten. A comparison of percentage composition was made by assuming that all stomachs were equally filled (Fig. 22). This method was probably valid when sample sizes were large but could have caused an upward bias of contents which normally occurred at low frequencies whenever sample sizes were small. For example, if species A comprised 50% of the stomach contents in one animal in a sample of ten, then the average percentage composition of that species during the period covered was 5%; if the sample size was one, the average percentage composition was 50%.

Overwintered seeds and berries (mainly bearberries and rosehips) were eaten in April and, with the addition of spring greenery, in May. By early June in 1969 and 1970 overwintered berries were either unavailable, suggesting poor growth in the previous years, or were not preferred. In 1971 overwintered foods were still found in the stomachs in late June.

Table 15. Frequency of occurrence of various foods in stomachs

Species	Common name	Portion eaten	Number of stomachs
Greenery			67
Arthropods			45
Arctostaphylos uva-ursi	bearberry	fruit, seeds	45
		buds, flowers	18
Rubus strigosus	raspberry	fruit, seeds	32
Shepherdia canadensis	buffaloberry	fruit, seeds	21
Rosa acicularis	prickly rose	hips	20
Vaccinium vitis-idaea	bog cranberry	fruit, seeds	19
Fragaria virginiana	strawberry	fruit, seeds	15
Lichens			10
Alnus crispa	alder	catkins	9
Viburnum edule	high bush cranberry	fruit, seeds	6
Taraxacum officinale	dandelion	seeds	5
Ribes oxyacanthoides	gooseberry	fruit, seeds	5
Geocaulon lividum	bastard toadflax	fruit, seeds	5
Unidentified			4
Prunus pensylvanicus	pincherry	fruit	2
Empetrum nigrum	crowberry	fruit	2
Ribes hudsonianum	black currant	fruit	1

N = 132

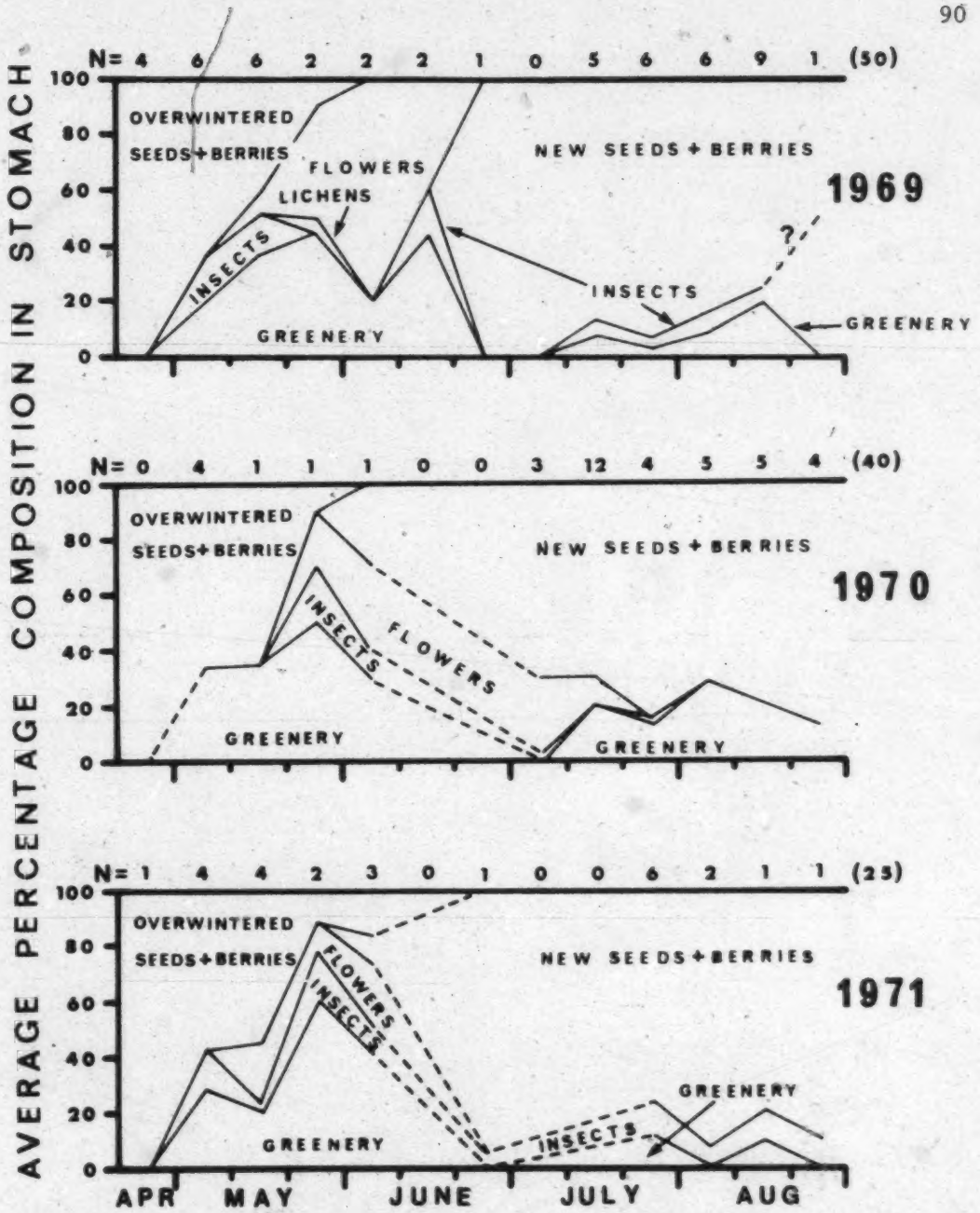


Figure 22. Changes in the average proportion of different foodstuffs in chipmunk stomachs in 10-day periods (1-10; 11-20; 21-end of month) during 1969, 1970 and 1971. N is the sample size.

Spring flowers were eaten and lasted until late June in 1969 and 1971, while they were still being eaten at the end of July in 1970. This suggests that a prolonged period of flowering and subsequent fruiting occurred in 1970. The appearance in the stomachs of new seeds and berries was later in 1969 (mid-June) than in 1970 and 1971 (late May to early June). Cool weather (Fig. 3) may have delayed the ripening process in 1969, and this could aid in explaining the prolonged appearance of overwintered berries in the diet in 1970. The apparently large crop of fruit in 1970 appeared in the stomachs earlier than in 1969, yet was still sufficient to last as overwintered berries well into the spring of 1971. Arthropods also appeared to play a smaller role in the diet in 1970 than in either 1969 or 1971. Differences in the habitats in which chipmunks were collected for autopsy (Appendix IV) do not explain the differences in stomach contents.

An index of similarity (MacFayden, 1957), calculated for the average percentage composition in the stomachs by adding the smaller of the two percentages for each 10-day period from Figure 22, shows:

1969 vs 1970: 939.2

1969 vs 1971: 1012.6

1970 vs 1971: 1037.8

This gives a gradation of dietary similarity such that 1971-1969-1970, or, 1970 was more dissimilar to 1970 than it was to 1969.

Juveniles first emerged in mid-July and the fruits available to them until the end of August and, obviously, in the collecting periods prior to hibernation, varied from year to year. Assuming that chipmunks are opportunistic feeders (Aldous, 1941; Snigirevskaya, 1962, 1964; Shubin, 1962; Forbes, 1966b; etc.), the fruits eaten by all animals at

that time each year reflect those readily available and also show considerable variation (Fig. 23). For example, buffaloberry was a common food in 1969 and 1970 but was entirely absent in 1971. A search in 1971 failed to reveal a single bush bearing berries although they were readily available in previous years. Both high-bush and bog cranberries were minor dietary elements in 1969 and 1970, but assumed greater importance in 1971. Strawberries were absent in 1971 and bastard toadflax was absent in 1969. Dandelion seeds and fruits of crowberry, pincherry and black currant made minor contributions in various years.

An index of similarity (MacFayden, 1957) reveals:

1969 vs 1970:	141.65
1969 vs 1971:	117.69
1970 vs 1971:	71.39

Again, the index provides an indication that 1970 was an exceptional year as the gradation was 1969-1971-1970, where the foods eaten in 1970 were more dissimilar to those in 1969 than to those in 1971, but late summer in 1971 was more like 1970 although the whole summer in 1969 was closer to that of 1970.

(iii) Cheek pouches

Seeds, which are part of the plant with the highest energy content (Golley, 1961), were found in the cheek pouches of 41 animals autopsied during the present study (Table 16). Most animals having seeds had collected only one species of seed when autopsied, but some pouches contained more than one species. Raspberry was the predominant seed collected in 1969 and was collected to a large extent in other years. Buffaloberry and strawberry were collected mainly in 1969, while

Figure 23. Average percentage composition in stomachs from animals collected between the times of juvenile emergence and the end of August.

Key:

a	*Rubus strigosus*
b	*Shepherdia canadensis*
c	Arthropods
d	Greenery
e	*Fragaria virginiana*
f	*Vaccinium vitis-idaea*
g	*Viburnum edule*
h	*Arctostaphylos uva-ursi*
i	*Ribes oxyacanthoides*
j	*Rosa acicularis*
k	*Peltigera fruticosa*
l	*Geocaulon lividum*

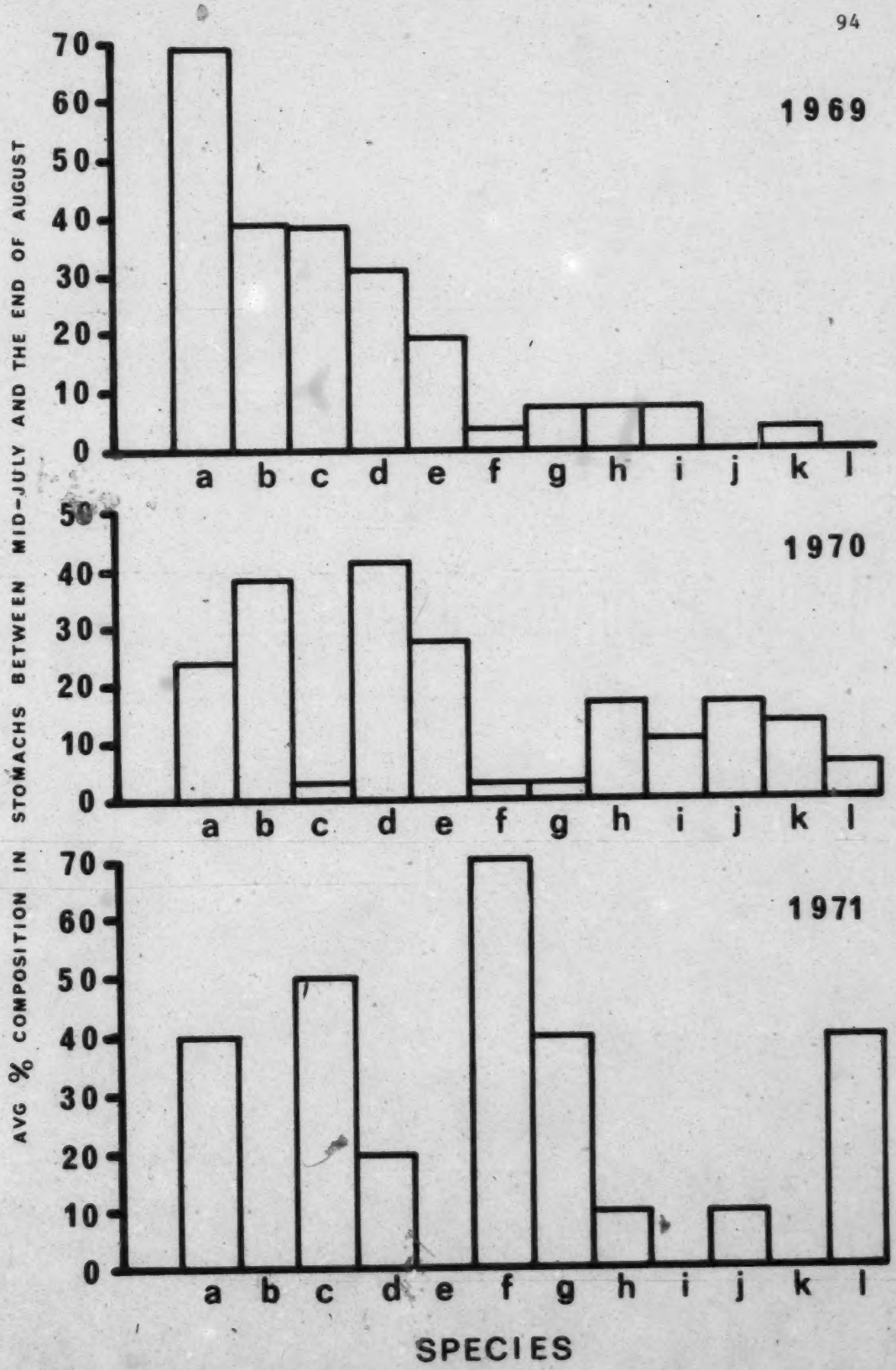

AVG % COMPOSITION IN STOMACHS BETWEEN MID-JULY AND THE END OF AUGUST
1969
1970
1971
0
10
20
30
40
50
60
70
a b c d e f g h i j k l
SPECIES

Table 16. Percentage occurrence of various seeds in cheek pouches during the study

Species	% of animals with seeds				
	1967	1968	1969	1970	1971
N	1	2	16	13	9
Shepherdia canadensis	100	50	25	23.1	0
Rosa acicularis	0	0	6.25	23.1	11.1
Geocaulon lividum	0	0	6.25	0	33.3
Carex sp.	0	0	6.25	0	0
Arctostaphylos uva-ursi	0	0	6.25	0	0
Lathyrus ochroleucus	0	0	6.25	0	0
Rubus strigosus	0	0	42.5	15.4	33.3
Viburnum edule	0	0	6.25	0	22.2
Fragaria virginiana	0	0	0	30.8	0
Ribes oxyacanthoides	0	0	0	7.7	0
Prunus pensylvanica	0	0	0	7.7	0
Potentilla fruticosa	0	0	0	0	11.1
Vaccinium vitis-idaea	0	0	0	0	44.4
Unidentified (seeds)	0	50	0	0	0

cranberries and bastard toadflax were major components only in 1971. These variations were similar to those found in the stomach contents in the latter part of summer (Fig. 23), again suggesting differences in the availability of fruits of different plant species each year.

Caloric values were determined for seeds of several species found in cheek pouches (Table 17). Assuming that seeds collected in late summer or fall are stored and used during the hibernation period (Howell, 1929; Criddle, 1943; Cade, 1963), differences in seed availability would affect the energy available for overwintering or the expenditure of energy necessary to ensure adequate supplies for winter. For instance, a greater weight of bearberry than bastard toadflax seeds would be required for winter in order to store the same amount of available energy. This problem would be increased by the fact that seeds of the former are so much smaller than the latter and more seeds by number as well as by weight would have to be collected. Unfortunately, no winter caches were located so that stored energy was not evaluated.

Cheek pouches were not used to the same extent throughout the summer (Fig. 24A). For comparison, stomach contents reveal the prevalence of overwintered seeds (mixed with the fruit of overwintered species) in early spring, followed by an increase in new seeds and berries in the second half of June (Fig. 24B). A definite lapse in time existed before those new seeds were found in the cheek pouches, as they were not found there until several weeks after the new seeds had begun to play an increasing role in the diet. Seed collection is probably tied to more than just availability, possibly not beginning until after the establishment of home ranges or until the initiation of a search image.

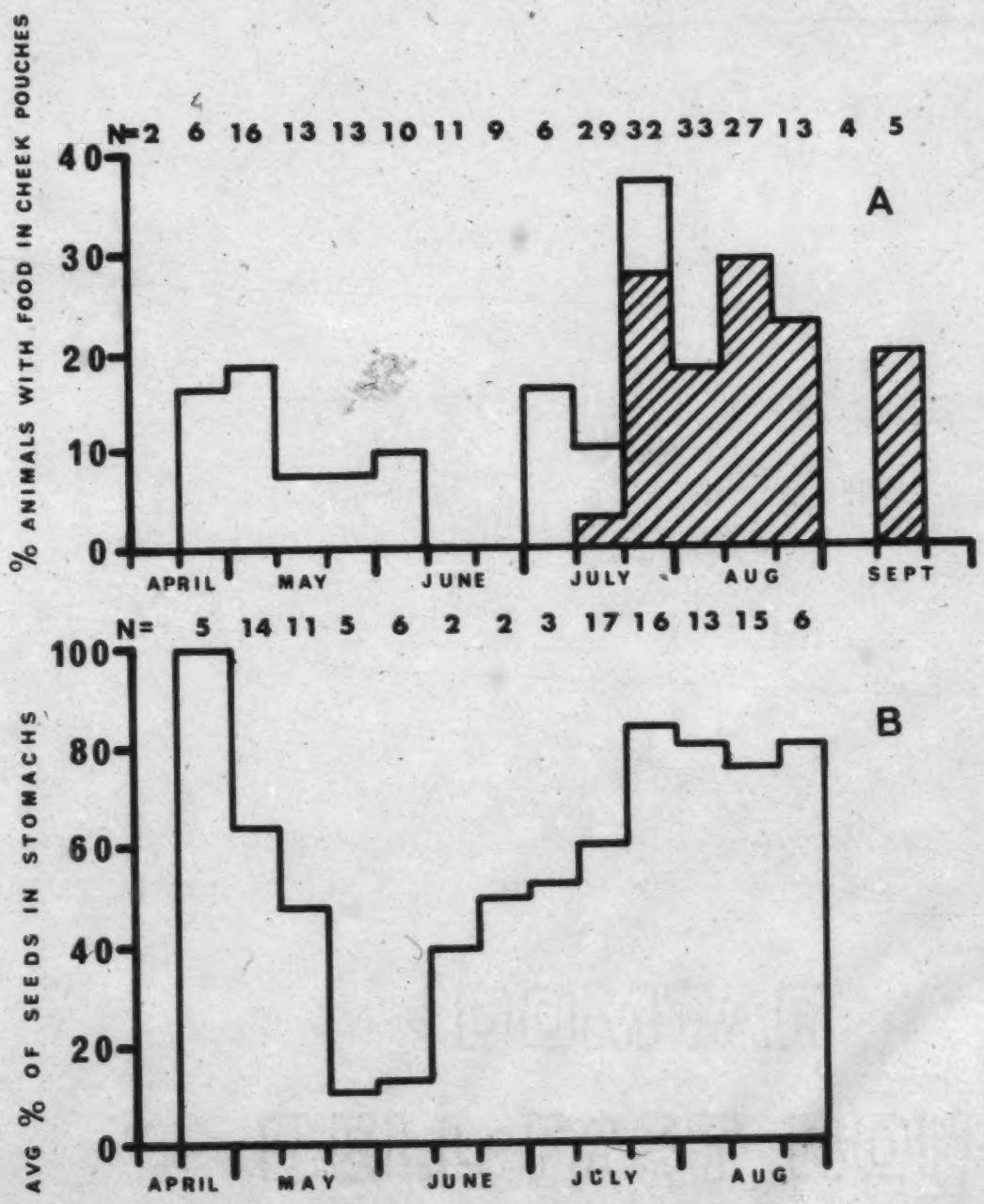
Approximately 20% of the autopsied population utilized their cheek

Table 17. Corrected calorific values (in kilocalories per gram) of air-dried, washed seeds of species found in the cheek pouches

Species	Samples				Average
	1	2	3	4	
Arctostaphylos uva-ursi	4.682	4.711	4.714	4.698	4.701
Arctostaphylos rubra	4.772	4.785	4.799	4.764	4.780
Rosa acicularis	5.060	5.055	5.055	5.057	5.057
Viburnum edule	5.244	5.252	5.173	5.173	5.210
Rubus strigosus	5.494	5.504	5.444	5.425	5.467
Vaccinium vitis-idaea	5.569	5.547	5.549	5.536	5.550
Geocaulon lividum	6.567	6.624	6.588	6.560	6.585
Average of all seeds					5.337

Figure 24A. Proportion of animals using cheek pouches by 10-day periods throughout the summer. Juveniles are indicated by the hatched portion. N is the sample size, pooled for all five summers.

B. Average percentage of seeds of all species in the stomachs of autopsied chipmunks in 1969, 1970 and 1971. N is the sample size.

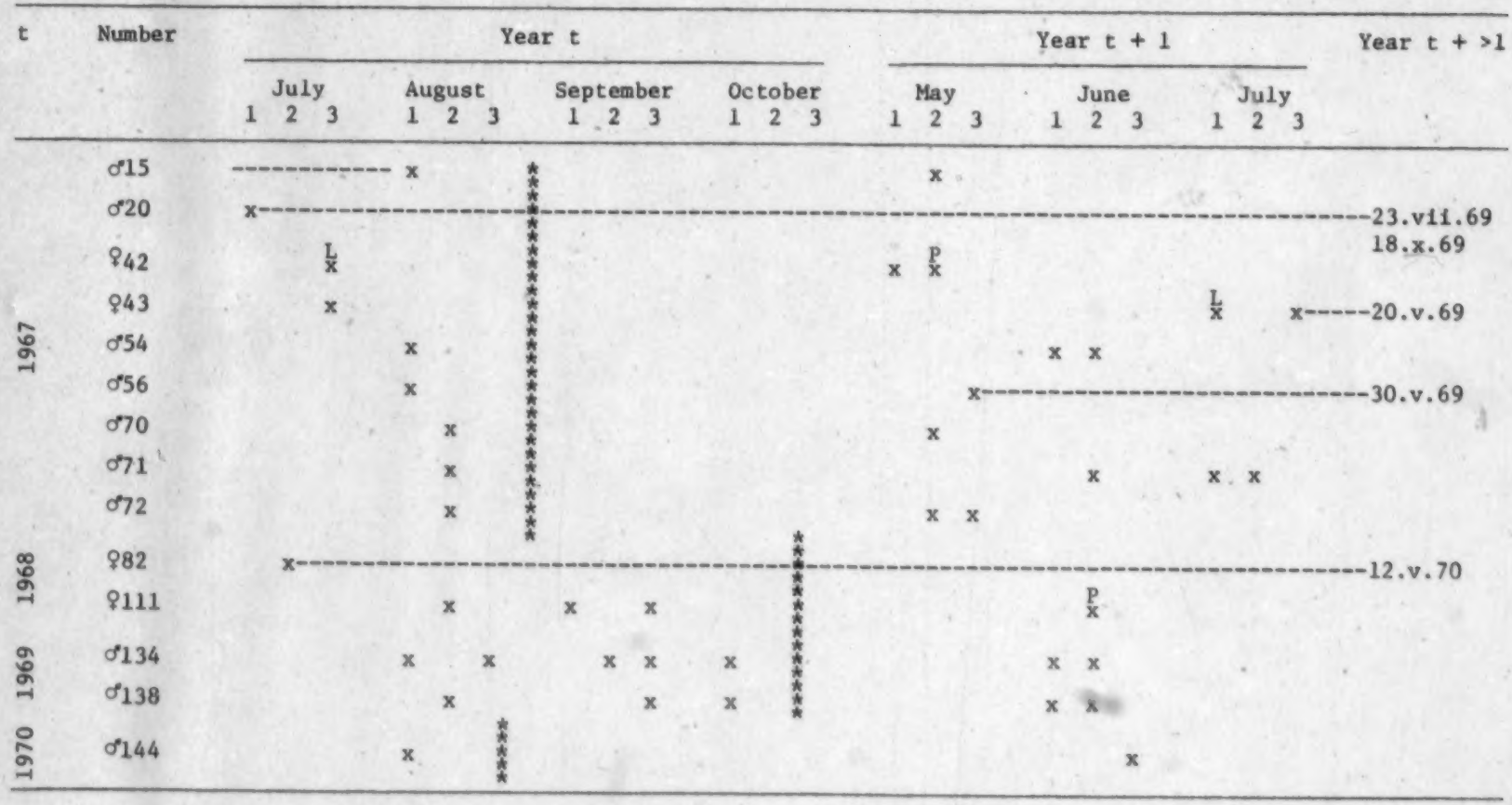

% ANIMALS WITH FOOD IN CHEEK POUCHES
N= 2 6 16 13 13 10 11 9 6 29 32 33 27 13 4 5
40
30
20
10
0
A
APRIL
MAY
JUNE
JULY
AUG
SEPT
N= 5 14 11 5 6 2 2 3 17 16 13 15 6
AVG % OF SEEDS IN STOMACHS
100
80
60
40
20
0
B
APRIL
MAY
JUNE
JULY
AUG

pouches in spring. The seeds carried at that time must have originated either from overwintered berries or from the remnants of winter hoards. In spring many places were observed where overwintered rosehips had been eaten; the seeds were missing and dried, overwintered pericarp was left uneaten. Although some of the signs may have indicated feeding by *Peromyscus*, several chipmunks were observed eating overwintered rosehips when snow was still on the ground in spring. Similarly, overwintered bearberries were eaten at that time. Cheek pouches may be used for conveying excess food to the burrows for later consumption as the animals are relatively conspicuous in snow and this behavioral mechanism may have survival value by decreasing predation and thermal stress. Stomach contents in spring occasionally included pieces of pericarp from *Rosa*, again indicating that overwintered berries rather than cache remnants were being eaten.

By late August and September slightly more than 20% of the autopsied population was again collecting seeds in the cheek pouches. Most animals in the sample from fall were juveniles; the proportion of overwintered animals collecting seeds at that time may well have been higher. Those juveniles with seeds in their cheek pouches may have been individuals that had settled into the population by establishing home ranges. Although some individuals of the "collecting type" would be expected to be sampled before they had a chance to fill their pouches, it seems that not all juveniles were attempting to hoard seeds during the time that samples were taken.

Marked animals recaptured following one winter were generally those individuals known to be on the plots in late summer, toward the ends of the trapping periods (Table 18). Those marked animals recaptured the

Table 18. Animals recaptured on the live-trapping plots in summers following their initial captures and recaptures. P = pregnant; L = lactating. Time periods are divided into 10-day spans with t representing the year of initial capture. Broken lines represent animals recaptured subsequent to the time spans shown in the table. x = one or more recaptures. Asterisks represent the ends of the trapping periods



following year as breeding adults (e.g. ♀ 42, ♀ 43) appeared to have established home ranges earlier in summer, while animals first captured nearer the ends of the trapping periods (e.g. ♂ 134, ♂ 138) did not seem to be in breeding condition (i.e. the testes were not evident). No chipmunks first captured on the plots after the beginning of September were ever captured the following spring, and two juveniles (♂ 110 and ♂ 118) first captured in mid-August and early September were found dead on the plots the following spring, apparently having died prior to snowfall. Animals recaptured more than one year following initial capture (e.g. ♀ 56, ♀ 82, ♂ 20) appeared to have only part of their "lifetime range" (Jewell, 1966) on the live-trapping plots and probably did not overwinter there. Thus, some animals appeared to have established home ranges by the end of August while others were probably searching for areas of non-harassment.

Soper (1964), referring to *E. minimus borealis* in Alberta, stated that "growth is surprisingly rapid; by early or mid-August most individuals are nearly adult size." Data from the present study support Soper's statement (Fig. 25) and show that "collectors" with seeds in the cheek pouches were usually heavier than "non-collectors" which had no seeds in their pouches.

Weather

Temperature

Mean summer temperature (Fig. 3) is positively correlated with the overall survival rate from one year to the next (Table 13) (Spearman's coefficient of rank correlation $R_s = 0.95$; $t = 4.308$; $P = 0.05$) (Fig. 26A). Lack of data precluded an exact evaluation of the precise nature of this relationship.

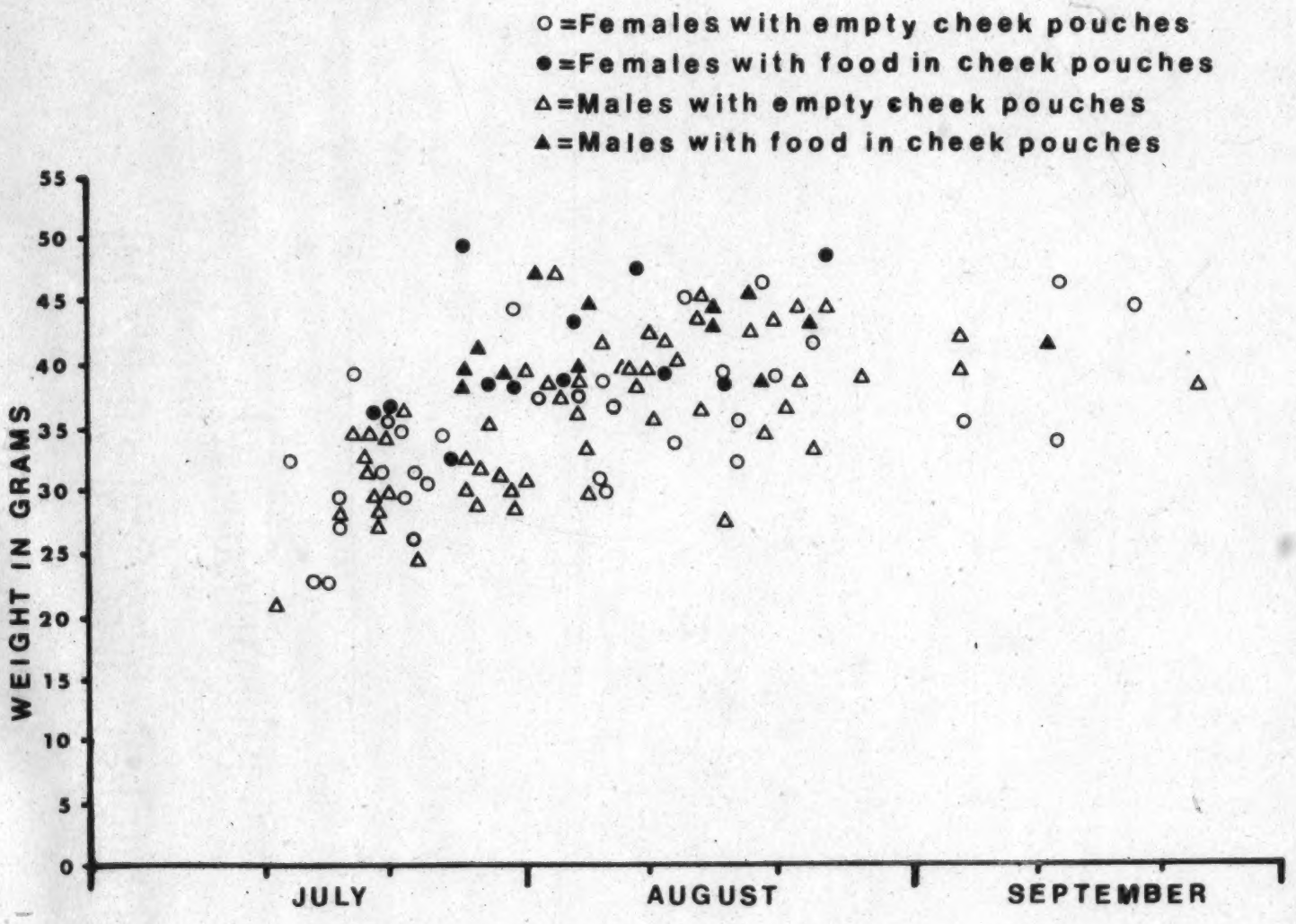


Figure 25. Weights of all juveniles captured during the study plotted against time.

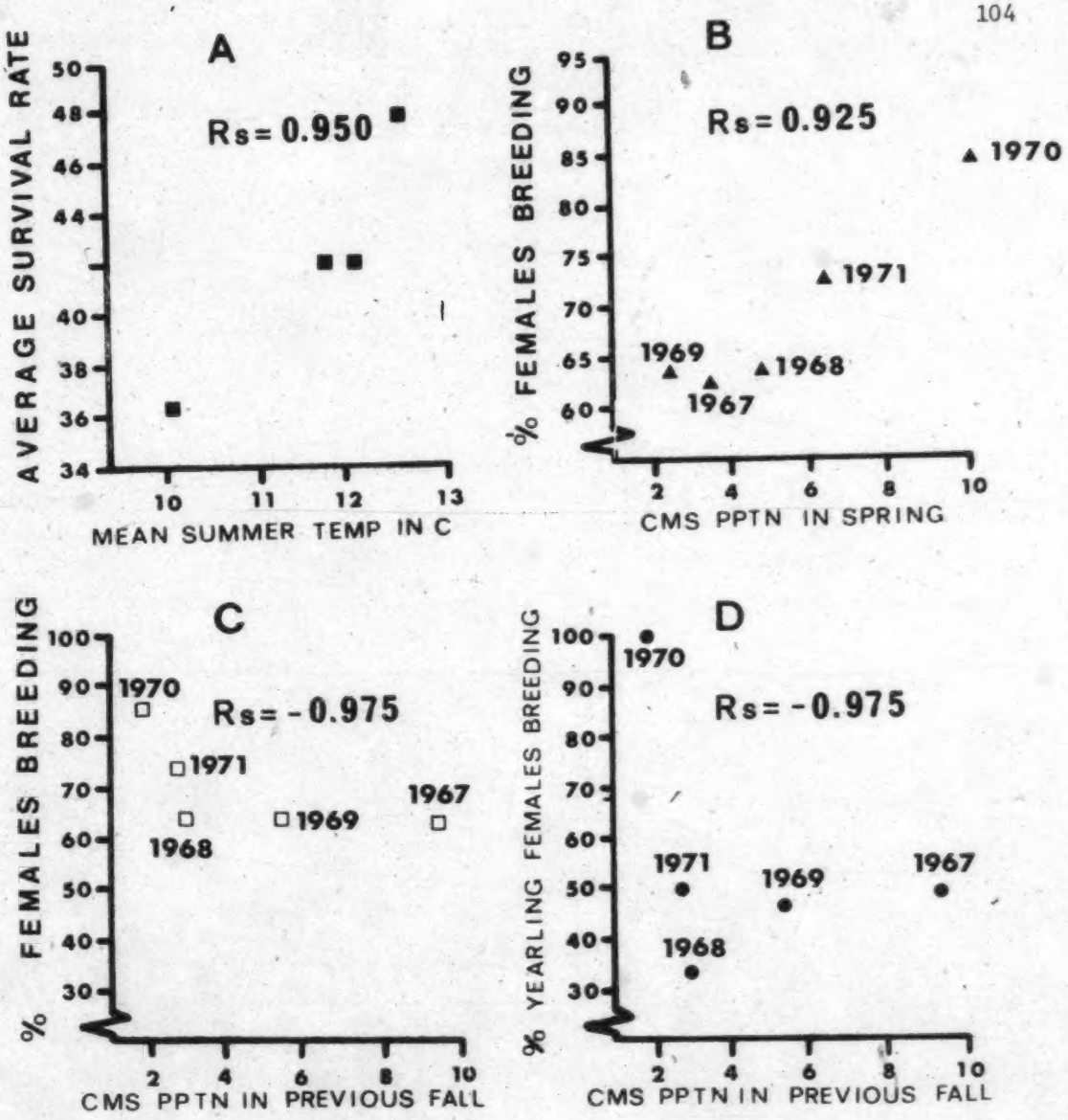


Figure 26. Correlation between temperature and average survival rate (A), spring precipitation and proportion of females breeding (B), autumn precipitation with proportion of females breeding the following spring (C) and proportion of yearling females breeding with precipitation the previous autumn (D).

Precipitation

The proportion of females participating in breeding is correlated with precipitation in spring (April and May). Figure 26B shows the nature of this significant relationships (R_s = 0.925; t = 4.217; P < 0.05). Precipitation in spring was largely in the form of "wet" (heavy, dense) snow or rain which provided sufficient soil moisute for rapid plant growth. An indication of a possible threshold in the percentage of overwintered females breeding following different spring precipitation recordings also exists so that the stimulus of moisture sufficient to promote adequate food supplies at the time of juvenile emergence could determine which females that are able to breed actually do so. This correlation is not in accord with previous results throughout the study and may have arisen because those years with good spring precipitation (1970 and 1971) followed ones in which autumnal food supplies were probably greatest (Fig. 22). Again, more years than were encompassed in the present study would have to be investigated in order to separate these two factors.

Autumnal (September and October) precipitation also affected the proportion of breeding females in the population the following year (Fig. 26C). This significant negative relationship (R_s = -0.975; t = 7.598; P < 0.01) indicates that in the years following wet autumns breeding is reduced, and the relationship was maintained when only yearling females were considered (R_s = -0.975; t = 7.598; P < 0.01) (Fig. 26D). An indication of a threshold also appears in Figure 26C and D, with that for yearlings at an apparently lower level, so that breeding in yearling females seemed to be lowered more by precipitation

in their first fall than was the case with older females.

Fruits and berries have normally matured by September and October so that food production was probably not influenced to any extent by precipitation at that time, although snow could have covered much of the food to make it unavailable. Chipmunk activity ceases in the rain (Dunford, 1972) and chipmunks were not observed during rainstorms in the present study, although they were seen to appear above ground before the foliage had died. Despite "intense activity in the fall" (in *T. striatus*) (Dunford, 1972), a high autumnal precipitation could prevent laying in of adequate reserves for winter, especially by animals which had not established themselves in the population prior to September as well as causing more mortality due to exposure among non-established animals. However, dry autumns occurred in years of good berry production during the years of the present study, and available food, rather than dry weather, was probably the major factor, although a longer study is needed in order to separate any effects.

General

Temperature and moisture are closely related and may even exert a synergistic influence upon the population. In general terms, the delayed spring followed by a moderately warm, moist summer in 1967 produced a low proportion of breeding females (Table 7) and a moderate overwinter survival rate (Table 13). Both breeding during and survival following the cool, moist summer of 1968 were poor. Breeding was again poor in the dry, warm summer of 1969 which followed a very dry spring, and survival was moderate. Following a spring with good moisture, summer

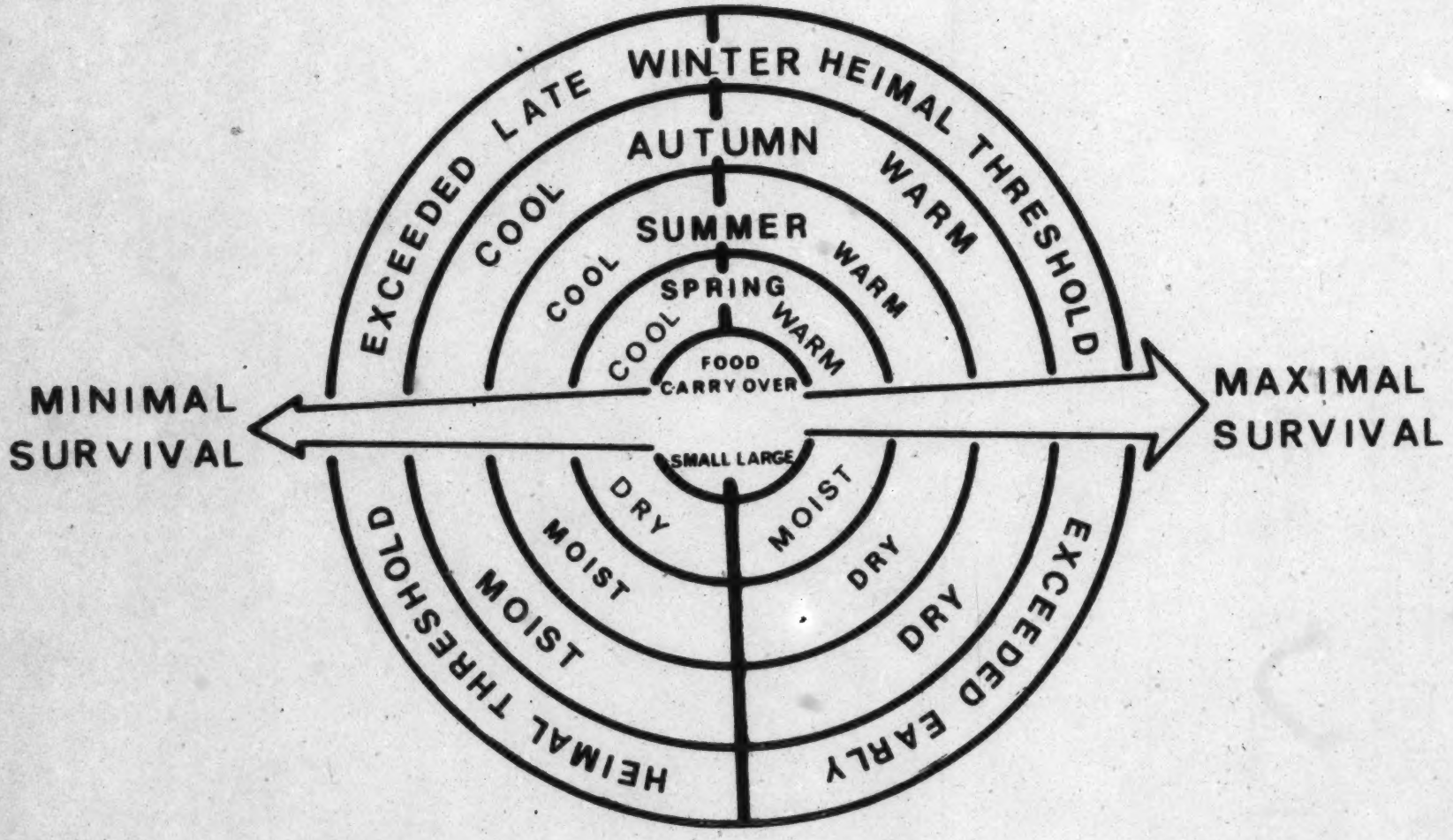


Figure 27. Effects of extrinsic factors on food production and survival of chipmunks.

was warm and dry in 1970, allowing both breeding and survival until the next year to increase. These factors have been summarized (Fig. 27) to show factors tending to maximize or minimize the chipmunk population.

Although overwintering survival following the warm, dry summer and moist spring of 1971 could not be determined, the proportion of breeding females was relatively high. By following weather trends from previous years it was possible to predict a high survival rate from 1971 to 1972; this was partially supported by the collection of three animals on Plot A in 1972 during spring, a period when very few animals were normally trapped (Fig. 7).

DISCUSSION

Any species which maintains itself at a constant population level probably does so by internal regulation (Lack's (1954b) "proximal limiting factors") such that numbers never become high enough to deplete the food resources ("ultimate limiting factors") in its environment. Such a premise would of necessity mean that the population would exist at a lower level than the maximum possible with available resources.

Consequently, in the present study a large area was sampled by autopsy. Logistic considerations prevented live-trapping over such an area and a much smaller area was selected for live-trapping in order to follow changes in gross numbers of chipmunks. In order to make the area live-trapped more comparable with that in which animals were collected for autopsy, consideration was afforded to the vegetative associations in which collections were made. For this reason live-trapping was conducted on three plots which, *in toto*, were reasonably

representative of topography and vegetative associations, determined from aerial photographs, within the larger area in which animals were collected for autopsy.

Populations studied within a large area almost certainly contain numbers of localized aggregations or "demes" (Anderson, 1970). Selection of a live-trapping plot with discrete borders (an enclosure or island) prevents distortion of ecological density by individuals which use that area for only part of their "lifetime range." Such a situation, however, although allowing a more critical analysis, can be misleading in that interactions between residents and dispersing or occasional immigrants are excluded and the resultant census, more accurate in itself, may not be representative of changes within the population of the general area surrounding one which is isolated. A live-trapping plot with non-restrictive boundaries will show inflated numbers due to occasional captures of animals actually resident outside those boundaries. This error was increased further in the present study because three plots were used and each one probably showed an increased population level and decreased temporal occupancy because of non-restrictive borders. Gross densities, rather than ecological densities, have thus been examined in both live-trapping and in the autopsied sample.

For this reason little emphasis can be placed upon differences between Plots A, B and C within any one trapping period. Annual differences between total numbers trapped (pooling numbers from all three live-trapping plots), however, are comparable provided that (1) interaction across borders is in proportion to numbers trapped and that (2) the error is of consistent intensity relative to population size. Estimation of the accuracy of these two conditions requires comparison with

non-available data from plots with discrete borders so that their validity during the present study was assumed. In terms of actual numbers, changes in population level on the plots are probably relatively correct although somewhat inflated. Similarly, mean times of occupancy and estimates of home range (although not minimum home range) are probably low in comparison with the data to be expected from plots isolated by restrictive boundaries. Pooling data from live-trapping plots, then, was considered justifiable in that the population under consideration was that in the general area sampled by autopsy and the total area live-trapped was considered representative of that larger environment.

Ideally, animals for autopsy should be sampled by collection during a predetermined periodicity (say, daily at an hour chosen at random) from a randomly selected locality within the large area sampled. This would preclude any biases for sex, age or breeding condition which could be introduced into sampling by differences in activity patterns or physiographic preferences. The autopsied sample was considered unbiased despite lack of temporal consistency in that any animal available was added. Localized demes were not oversampled as no concentration of collecting effort was enforced upon any particular locality or vegetative association within the larger area and no particular time span appeared to bias collection of any class of animal (Appendix IV). Breeding in females was evident from placental scars long after breeding ceased, and no bias was introduced into estimations of the proportion of over-wintered females breeding each year by differences in collection times or locations. Breeding in four-year-old females was almost certainly

the reason for an increased proportion of breeding in 1970 (Table 7), but this was regarded as an intrinsic feature of the population rather than a sampling error because those females were collected with no sampling emphasis on either time or locality.

The premise that the population live-trapped each year (pooled for all three plots) is a realistic indicator of trends in the numbers of chipmunks in the whole area (sampled by autopsy) can be tested by constructing a theoretical population using data from the autopsied sample. The sex ratio for each age class is assumed to be parity because of small sample sizes and because the overall sex ratio was parity (Table 7). Embryonic contributions from each age class each year are known (Table 10) and survival during weaning has also been calculated (Table 12) so that the contribution to the population from each age class each year can be added.

For example, in 1967:

Contributions by juveniles = 0

Contributions by yearlings = 2/4 x 0.5 x 5.0 = 1.25

where 2/4 = proportion of females breeding

0.5 = proportion of females in population

5.0 = number of embryos per breeding female

Contribution by two-year-olds = 1/1 x 0.5 x 5.0 = 2.50

Contribution by three-year-olds = 2/3 x 0.5 x 5.0 = 1.67

Using the annual contributions from each age group for each year for a single year and the mortality between consecutive age groups in consecutive years (Table 13), it is possible to follow the size of a theoretical population beginning with 71 animals in 1967.

Year	Juveniles	Age 1	2	3	4	Total
1967	18.750	7	2	3	0	30.75
or, for a population of 71:						
1967 (mortality)	43.29	16.16	4.62	6.93	0	71
1968 (natality) (mortality)	35.57	15.71 (10.48	10.05 21.35	1.25 3.74)	0	62.58
1969 (natality) (mortality)	27.91	9.87 (9.42	6.56 9.84	3.93 8.65)	0	48.28
1970 (natality) (mortality)	30.10	5.75 (13.41	4.30 6.45	1.54 3.46	3.13 6.78)	44.82
1971 (natality)	21.32	9.20 (10.73	2.26 6.21	3.15 4.73)	0	35.93

A considerable difference exists between these figures and the numbers actually trapped on the plots (Fig. 28). However, all trap-deaths were included in the autopsied sample (Table 3), and the age of those animals has been determined. Thus, a model similar to that above can be constructed from which the number of animals that died during trapping can be removed at a time relative to their contributions to the juvenile cohort (i.e., trap-deaths occurring before the emergence of juveniles are considered to have failed to contribute progeny). This shows the effect on the overall population of mortalities equivalent to the trap-deaths:

In 1967 4 yearlings died before making contributions (i.e., 4 x 1.5 = 6.0 juveniles were not contributed).

		Age				
Year	Juveniles	1	2	3	4	Total
1967	37.29	16.16	4.62	6.93	0	65
or, for a population of 71:						
1967	40.73	17.65	5.04	7.57	0	71
(traps)	1	1				
continuing population	39.73	16.65	5.04	7.57	0	
(mortality)						
1968	30.90	14.42	10.35	1.36	0	57.03
(traps)		4	1			
		10.42	9.35	1.36	0	
(natality)		(6.95	19.87	4.08)		
(traps)	5	1				
continuing population	25.90	9.42	9.35	1.36	0	
(mortality)						
1969	18.36	7.18	3.93	3.66	0	33.14
(traps)		1	1			
		6.18	2.93	3.66		
(natality)		(5.90	4.40	8.05)		
(traps)	5	2				
continuing population	13.36	4.18	2.94	3.66	0	
(mortality)						
1970	12.51	2.75	1.82	0.69	2.91	20.69
(traps)		1			1	
		1.75	1.82	0.69	1.91	
(natality)		(4.08	2.74	1.54	4.15)	
(traps)	5					

Year	Juveniles	Age 1	2	3	4	Total
continuing population (mortality)	7.51	1.75	1.82	0.69	1.91	
1971 (traps)	6.58	2.30	0.69	1.34	0	10.90
(natality)		(2.68	1.89	2.01)		
(traps)	6	2	1			

When these trapping mortalities are subtracted from the theoretical population levels, adjusted levels for the initial 71 animals (from the general population) are very close to those observed on the live-trapping plots (Fig. 28). The only real deviation occurs in 1971 when the theoretical population declined further although the number of animals trapped on the plots increased. A possible explanation is that the population on the live-trapped plots had been so depleted by trap-deaths that, although the total population itself was at a low level, the plots were at an even lower level and afforded added opportunities for colonization or expansion of home range by animals from outside the plot's borders. The removal of animals from the plots in 1971 may well have increased intrusions. Another possibility is that the numbers recorded are inaccurate at such low levels. In any case, the difference between the theoretical and observed populations can largely be explained in terms of trap-deaths.

A further method of correcting for trap mortality involves the addition each year of the contribution that would have been made to the actual population on the plots had those deaths not occurred. Allowing for the time at which mortality occurred relative to the breeding

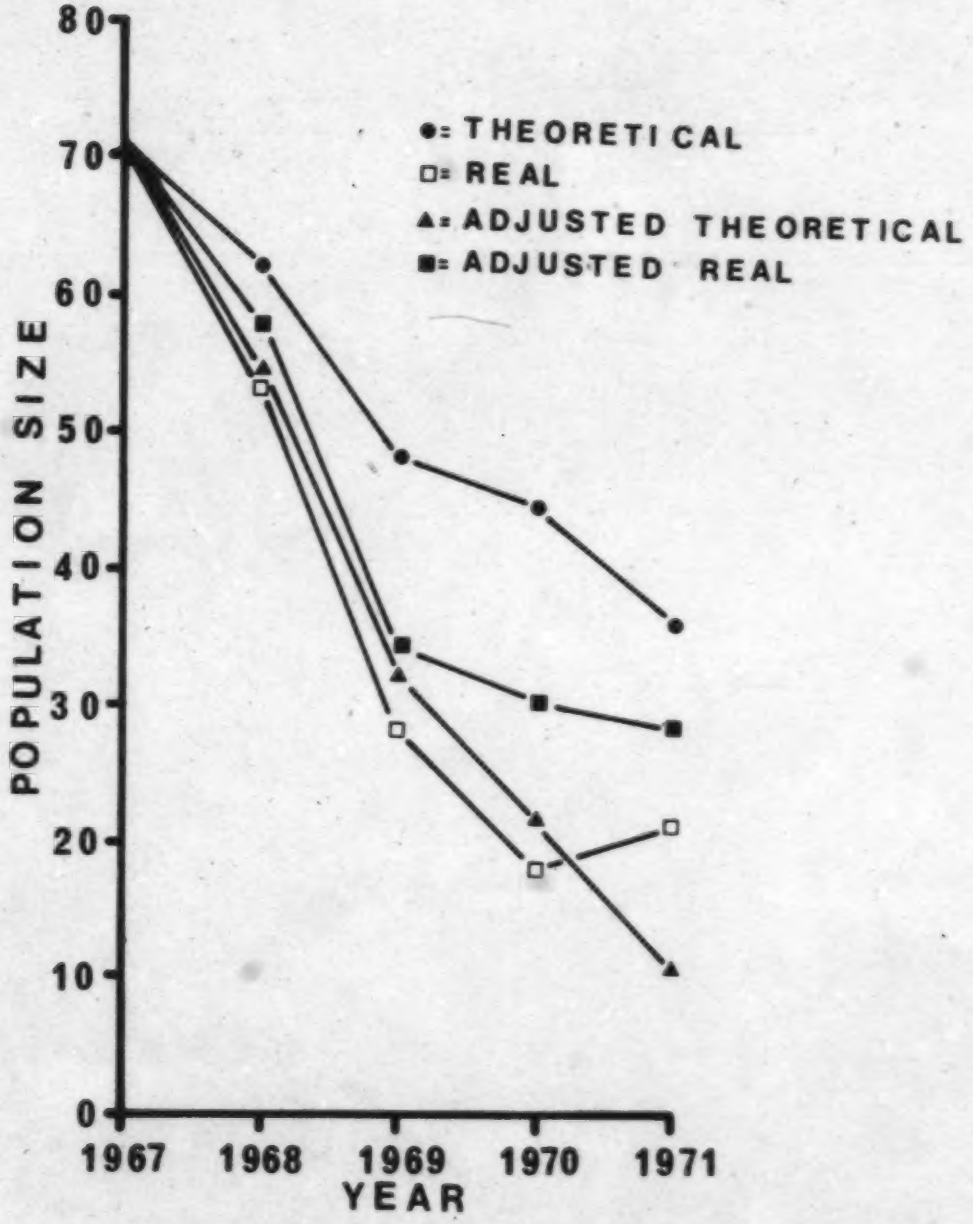


Figure 28. Real and adjusted (for trap deaths) populations on the plots throughout the study and theoretical population levels on the plots from autopsy data (with and without adjustment for trap deaths).

season, the adjusted populations on the plots should have been: 1967, 71; 1968, 57.12; 1969, 34.10; 1970, 30.79; 1971, 28.24 (Fig. 28). This adjustment does not produce an exact coincidence with the theoretical population although compensation for trap-deaths does cause the real population on the plots to approach the theoretical one.

The population of *E. minimus* at Heart Lake is unstable over a short period of time, although long-term stability is to be expected in order that extinction should not occur. Changes in theoretical populations coincide closely with those on the plots, so that the live-trapped sample appears to be a realistic indicator of population trends.

The decline in chipmunk numbers was not synchronous with declines in red-backed voles or with deermice, although data relating to population size near Heart Lake are scant for *P. maniculatus*. No population maxima have been observed for either *Clethrionomys* or *Peromyscus* since 1966 (Fuller, 1969). Following a decline in 1967 and a low in 1968, August numbers of *C. gapperi* have been essentially constant from 1969 to 1972 (W. A. Fuller, pers. comm.).

With a litter size of approximately six, a sex ratio of parity and a possibility of three litters, the first two of which could also reproduce that year (Fuller, 1969), one overwintered female *C. gapperi* could produce 36 female descendants in one year. *P. maniculatus*, however, only produces two litters per summer near Heart Lake (Fuller, 1969), so that 18 female descendants could be produced by one overwintered female during a favorable summer. If breeding occurred, one overwintered female *E. minimus* could only produce 2.2 to 2.5 female offspring. Response, in terms of population size, to favorable conditions should thus be more

rapid in the "annual" *C. gapperi* and, to a lesser extent in *P. maniculatus*, than in "perennial" *E. minimus*.

A further factor which could affect synchrony in sympatric populations of *E. minimus*, *P. maniculatus* and *C. gapperi* is differential survival, probably related to their different modes of winter life. Temperature fluctuations in chipmunk hibernacula prior to the attainment of the heimal threshold (Fig. 18) were probably less than those at the soil surface. Chipmunks appeared to be affected to a lesser degree (survival rates were highest from 1970-71, Table 13) than cricetines in the subnivean environment by late attainment of the heimal threshold in 1970. Mortality throughout winter, as suggested by Fuller *et al.* (1969), could have prevented any increased population of *C. gapperi* from surviving to reproduce in 1971, while the apparently well-nourished population of *E. minimus* in 1970 survived in hibernacula to increase in numbers in 1971. Thus, lack of synchrony in population changes in sympatric species does not necessarily exclude extrinsic causal factors, but may be a reflection of differences in life history.

Tevis (1955) found that *E. speciosus*, *E. townsendii* and *E. quadrimaculatus* accumulated fat in the fall, although Jameson and Mead (1964) showed that there was a decline in body weights in October in *E. speciosus* and *E. quadrimaculatus*. A vernal weight loss followed by a gain in fall was found in *T. striatus* by Panuska (1959). No autumnal accumulation of fat was found in *E. minimus* in Minnesota (Forbes, 1966c) or Alberta (Sheppard, 1968), or in *E. amoenus* in eastern Washington (Svihla, 1936; Broadbooks, 1958). Lipid deposition was not measured in the present study but no accumulation of fat was evident in autumn.

A "cycle" of body weights may be indicated (Fig. 10), but the frequency can not be determined as it probably exceeds the period of this study, as does any "cycle" of population size in the chipmunks near Heart Lake. Mean body weights, which were not merely a function of the time of collection (see Appendix IV), were high at the population maximum in 1967, a situation similar to that found by Krebs (1964), but they also increased in 1971 in a population that was increasing but had not attained a density close to that of 1967. This may be explained by the postulate that growth in juveniles was more rapid in 1966 and 1970, as the production of fruit in those years was larger than in other years. The survivors would benefit again from the large carryover of berries in the springs of 1967 and 1971. Thus, the yearlings in the latter years would be larger than in all other years. The regular increase in spring temperatures in May 1967 and 1971 (Fig. 3) may also have allowed a greater nutritive value for overwintered fruits in those years which could have contributed further to spring growth. Other years during the study were characterized by fluctuating temperatures in early spring.

Although annual differences in population structure were small (Fig. 12), that cohort born in 1966 appeared to be stronger than all others and was the only one to reach four years of age. Other cohorts showed a progressive mortality each year such that no individuals that had attained four years of age appeared in the samples. The cohort born in 1964 (i.e., three years of age in 1967) also seemed to be slightly larger than most others (Fig. 12) although weather factors in 1964 did not favor fruit production (W. A. Fuller, pers. comm.). That this cohort appeared larger than most others may be an artifact of small sample sizes

as the difference in numbers autopsied between two- and three-year-olds was only one (Table 7). Shtil'mark (1967) found a similar strong cohort of *E. sibiricus* in USSR and related it to a copious food supply when the cohort was juvenile. Dyke (1967) reported that 1966 was the best year for berry production near Heart Lake from 1964 to 1968 inclusive, so that the strong cohort born in that year may have had an increased food supply when it first emerged and again in spring 1967.

Potential recruitment would be increased if more than one litter could be raised each year. Sheppard (1969) stated that "chipmunks in western Alberta are restricted to one breeding season and one litter per year," although two litters have been recorded at lower latitudes (Manville, 1949; Negus and Findlay, 1959). Three litters were born to a pair of captive *E. minimus* in a single season in Manitoba (Criddle, 1943), although the first two were lost soon after birth, sothat the potential for producing more than a single litter would seem to be present, at least in captivity. The present study, however, is in agreement with Sheppard's limit of a single breeding season and a single litter each year (Fig. 11), while recent work (Smith and Smith, 1972) has confirmed the presence of two breeding seasons in *T. striatus*.

Tevis (1955) and Sheppard (1969) recognized sexually mature males during the entire summer by their enlarged testes which became flaccid in late summer in contrast to the smaller, firmer testes of sexually immature males. However, after mid-May, Venhuizen (1970) could not distinguish males which had bred from those which remained immature and no separation was possible in the present study.

It appears that a "critical stage of development" was not attained in the smaller (non-breeding) yearlings in the present study.

The breeding season at Heart Lake is restricted in length (Fig. 11), and differences in size could arise if some yearlings failed to "develop" sufficiently as juveniles before overwintering. Sadleir (1969) reviewed the effect of nutrition on puberty in many species of mammals and demonstrated that sexual maturity is frequently delayed when food supplies are low. Food supply was found to determine death rate and, possibly, birth rate in isolated populations of white-footed mice, *Peromyscus leucopus* (Bendell, 1959) while Gunson (1970) showed that reproduction in beaver *Castor canadensis* was poorer in low quality habitats. Foa (1900) first showed that adequate somatic development was necessary for reproductive maturation, and further work in this century has demonstrated that initial production of gonadotropins follows sufficient body growth (for review, see Parkes, 1966). Adequate somatic growth is therefore necessary before reproduction can occur and Vaughan's (1969) concept of the need for sufficient "development" before reproduction can occur in chipmunks is another expression of what Sadleir (1969, p. 4) terms the "law of puberty."

Determination of the limits of home range was inconclusive, but the data suggest that overlap occurs in both sexes. Females appear to occupy areas of at least 0.4 ha while males possibly range over at least 1.2 ha, and probably occupy larger areas which extend off the plots. Martinsen (1968) showed a mean summer home range for adult female *E. minimus* in Montana of 1.1 ha while Broadbooks (1958) found a mean home range of 0.9 ha for female *E. amoenus* with a mean overlap of 21.7%

and a mean home range of 1.5 ha for males. Storer *et al.* (1944) estimated that *E. quadrimaculatus* females had home ranges of 0.5 ha and males 0.9 ha. Both Manville (1944) and Jackson (1961) estimated home ranges at less than 0.4 ha in *E. minimus*, but considered their estimates low.

Rather than being directly density-dependent, the proportion of breeding females each year seems to be a function of home range size in that the percentage increases with decreasing population size only when the population falls below a "critical density" shown by the sharp break in Figure 14 (i.e., when the area is not fully occupied). The "critical density" of approximately 24 animals on the plots (12.4 ha) allows a minimum home range of approximately 0.5 ha which is in close accord with the average minimum home range determined in the present study for six animals (0.6 ha) and values in the literature. Prenatal mortality was not affected by population size (Table 11), suggesting that breeding females are not unduly affected by their external surroundings once copulation has occurred, or that they are normally located in more favored areas. However, small sample sizes necessitated pooling of data and local densities were not known although no effect of local variations in vegetation distribution was apparent (Appendix IV).
The proportion of juveniles in the population does not increase above a "critical density" indicated by a less precise threshold (Table 4) and is directly proportional to the percentage of females breeding (Table 12). An apparent threshold in Figure 26B, C and D also supports the contention that recruitment is regulated by the proportion of females with suitable home ranges in that a certain percentage of the population appears to

survive and reach sexual maturity regardless of temperature and precipitation.

Temperature *per se* is unlikely to be the proximate cause of mortality (Fig. 26A) as chipmunks can, and do, evade inclement weather by seeking refuge in their burrows (Dunford, 1972). Maturation of fruits and berries was probably retarded in cool summers so that less food would be available in autumn and winter. Lack of food for some individuals, particularly juveniles, could prevent breeding the following spring in *E. minimus*. Insufficient food would be a factor if a suitable home range was not established in an area with adequate resources. Carrick (1963) showed that the Australian magpie *Gymnorhina tibicen* was unable to breed in the absence of a territory, although sufficient food was available to the "flock" outside the territories. Bergstedt (1966) stated that "territories with sharp and well-maintained borders do not occur in small rodents," and behavioral studies on chipmunks support this assertion because aggressive behavior has been recorded only near the dens (Gordon, 1938; Broadbooks, 1970a; Dunford, 1970; Brown, 1971). The stimulus, independent of food, of actually inhabiting a home range, meaning an area of relative non-harassment, could be responsible for breeding the following spring in *E. minimus*, although nutritional factors are difficult to separate from that possible stimulus in field studies.

No significant difference existed in the embryonic contributions each year of those females which bred (Table 10), so that all females occupying home ranges which provided nutriton adequate for both survival and the somatic development necessary before breeding can occur, probably did breed and did so to a constant extent. Larger breeding

populations presumably follow autumns when marginal home ranges provide the resources necessary for survival and reproduction the following spring. It is possible that the proportion of breeding males followed a similar pattern to that of the females, with increases in 1970 and 1971, although no data are available.

Andrzejewski *et al.* (1967) found an association between body weight and size of home range in bank voles and suggested a dominance hierarchy. The heavier "dominant" animals in their study and in other studies (Brown, 1966; Wolfe, 1966) may well have been those which occupied home ranges capable of providing sufficient nutriton to allow reproduction. Somatic development may be genetically controlled (i.e., a fast-growing and a slow-growing genotype may be present) or may be solely dependent upon nutriton. The correlation between maturation and body size or maturation and cranial size can now be explained in terms of home range in that those animals with no home range in late summer and autumn may not have gained enough energy for sufficient somatic development before hibernation. It is to be expected that natality would cause an excess of animals, many of which could not gain one of the (approximately) 24 home ranges available on the plots.

Christian (1971) found that field voles *Microtus pennsylvanicus* in which maturation was inhibited showed no evidence of having been attacked or having fought, and suggested that changes in the rate of maturation with density could explain differences in the tolerance of young males by older males. Should such a behavioral difference occur in *E. minimus*, a reserve portion of the population could be relatively protected from aggression by mature animals with established home ranges

and yet be available for reproduction once the population declined to such a level that there were vacant home ranges available for colonization. The reserve portion would comprise animals that managed to establish a home range in late fall. Suggestions of increased mobility by juveniles in late August (Fig. 17) support the contention that a proportion of the population actively seeks out areas in which to settle.

It is proposed that in August juveniles suffer one of three fates. Those that have established a home range prior to that time and have become "collectors" will form the breeding yearlings of the following spring. Those "non-collectors" that attain a marginal home range or an adequate home range between August and October may lay in sufficient stores to survive winter and emerge as non-breeding yearlings because they have gained sufficient energy for survival but not enough for the somatic development necessary for breeding. Those that fail entirely to establish a home range fail to survive the winter. During the course of the second summer most non-breeding yearlings will establish an adequate home range, but some few may manage to survive a second winter under marginal conditions and remain immature as two-year-olds (Fig. 29). A regulatory mechanism such as this would result in a constant population size unless the number of home ranges available was also variable. Considerable variation in fruit production has been demonstrated in the present study (Figs. 22 and 23), so that resources available to the chipmunks show marked fluctuations between years. It is proposed that in years of good berry production a greater number of adequate ranges will be available and that the number of marginal ranges will also increase, resulting in increased survival until the following year

(especially in the juvenile cohort) as well as an increase in the proportion of breeding animals.

Reasons for differential survival in the young cohorts favoring females are unclear (Fig. 13). Males have larger home ranges and may need more food than females. Sellers *et al.* (1950) showed that male rats *Rattus norvegicus* excrete more protein than females, probably because of their hormonal balance, and are thus less efficient in using available nutritive resources. Unless they overlap more, their larger home ranges limit the number of males of *E. minimus* occupying a predetermined area and may also bring them into more frequent aggressive contacts with other individuals. Predation is also more likely in animals with wider ranges as it may be more difficult to become familiar with the details of a larger range than of a smaller one. This possible mortality factor would likely affect younger animals without home ranges or with incompletely established home ranges to a greater extent than those already "settled."

Cade (1963) estimated energy available during hibernation for three species of *Eutamias* and concluded that they were "more dependent upon storing food sufficient for the winter season in the hibernaculum than

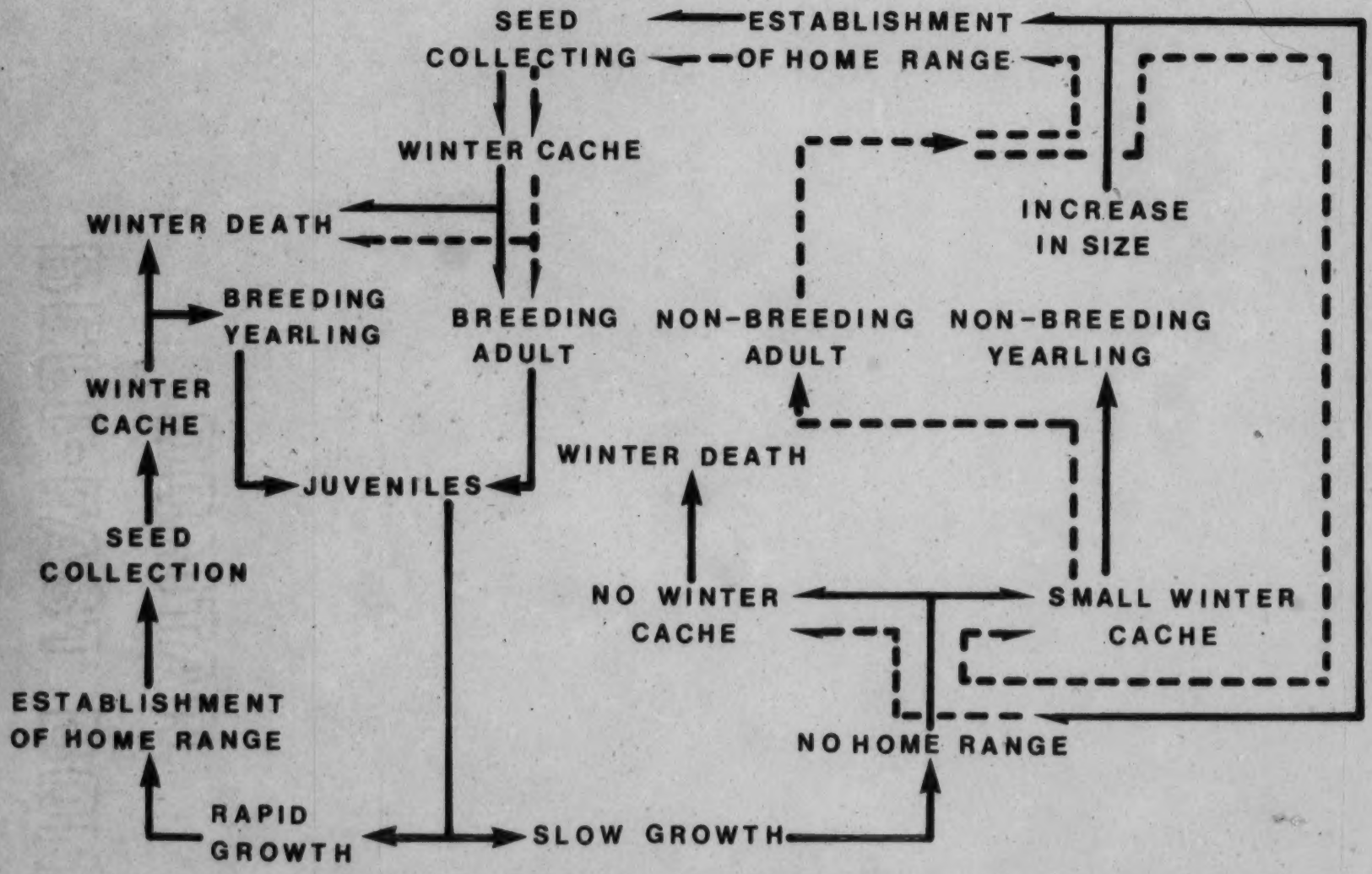


Figure 29. Schematic representation of the hypothesis proposed to explain changes in population size of *E. minimus borealis* near Heart Lake.

on drastically reducing metabolic rate and energy requirements by means of deep hibernation." Using Broadbooks' (1958) data from central Washington, Cade decided that starvation was unlikely and Broadbooks (1970a) agreed with that deduction because of high overwintering survival rates. However, using a more detailed list of caloric equivalents (Cummins and Wuycheck, 1971) and a 70% efficiency in assimilating the food (Brody, 1945), the net energy available for assimilation by *E. amoenus* in Broadbooks' (1958) three caches was 264, 619 and 480 kilocalories. It is thus unlikely that the first cache contained sufficient energy for overwintering survival (see p. 82).

Engels (1947) recorded volumes but not weights of caches in the hibernacula of *T. striatus*. Criddle (1943) found three winter hoards of *E. minimus* in southern Manitoba with weights of 528.5 g, 465 g, and 799 g. Assuming equal weights of all components within each cache, the digestible caloric values can be estimated with the aid of tables in Cummins and Wuycheck (1971), Grodzinski and Sawicka-Kapusta (1970) and Brody (1945). Hibernation periods in southern Manitoba are more comparable than in central Washington with those from Heart Lake, and the assimilatable energy values of the caches described by Criddle (1943) were about 1850, 1530 and 2730 kilocalories. Two caches excavated in September by Snigirevskaya (1964) in Siberia contained approximately 6100 and 5300 digestible kilocalories. Shtil'mark (1963) reported that Siberian chipmunks hoarded two to three kilograms of stonepine seeds which would have a digestible energy content of 8500-13000 kilocalories (Grodzinski and Sawicka-Kapusta, 1970; Brody, 1945).

Caches of *E. minimus* (Criddle, 1943) appear to contain sufficient

energy reserves for overwintering survival provided that hibernation occurs, while *E. sibiricus* seems to store sufficient food for overwintering without hibernating. However, *E. sibiricus* does exhibit hibernation with periodic arousals throughout the winter (Jaeger, 1969). Mortality due to food depletion can not be eliminated as a strong possibility in some (one, at least) of Broadbooks' (1958) *E. amoenus*, and may have occurred during the winter at Heart Lake in animals which had not established home ranges.

Graves (1971) reported that "hibernation did not occur in animals with low cache amounts" (in *T. striatus*). Non-hibernating chipmunks require a much greater amount of energy than individuals in hibernation (p. 78) and, if smaller cache amounts were available to them while their requirements were increased, the probability of mortality would be greatly increased. Mortality during the overwintering period, then, is a distinct possibility where home ranges have not been established.

Telegin (1957) and Shtil'mark (1967) postulated that breeding was controlled by the amount of energy remaining in the caches in spring, with those animals which had depleted their winter stores having insufficient energy available for reproduction. This may well occur at Heart Lake, where those individuals with inadequate home ranges may deplete their caches for survival and not be able to breed. However, spring food appears to be gleaned from above-ground overwintered berries rather than from caches. If the berry supply had been depleted during hoarding in marginal ranges, there would still be an energy shortage in spring.

Many of the classical theories of population regulation can be

reconciled in the present hypothesis (Fig. 29), as each theory seems to have concentrated on a different level of change within the population. Elton's (1924, 1942) suggestion that "climatic variations" are responsible for synchronous, single-species population fluctuations over wide areas can be explained, with "production years" (Kalela, 1962) occurring when climatic conditions favor survival and reproduction on marginal home ranges. Food supply, as suggested by Lack (1954b), is probably the factor by which these climatic variations largely manifest their effects upon the population (although inclement weather can probably nullify the beneficial effects of copious food resources as appeared to occur in *C. gapperi* at Heart Lake in winter 1970-71). The concept of "survival ranges" and "colonization ranges" for demic populations (Anderson, 1970) appears to function at the individual level in *E. minimus* with non-breeding "colonizers" from marginal ranges having additional opportunities following somatic development to become part of the breeding "survivors." Chitty's (1967) concept of genetic differences in behavior can also be reconciled, with those individuals of a more aggressive genotype establishing themselves in the more favorable areas and the less aggressive genotype settling marginal areas or vacancies left by the deaths of more aggressive animals. The less aggressive genotype would be retained in the population by the ability in animals of that genotype to breed for the first time at an older age. Stressful aggression from older animals would be avoided by retention of immature status (Christian and Davis, 1964; Christian, 1971). "Dominance" of heavier animals over lighter individuals (Brown, 1966; Wolfe, 1966; Andrzejewski *et al.*, 1967; Friesen, 1972) can also be explained if animals with established home

ranges are normally more aggressive because of either their larger size or their predominating genotype.

Food has been described as the "ultimate limiting factor" for populations, although "proximate limiting factors" may come into play and prevent its expression (Lack, 1954b). Heart Lake is located near the northern limit of the range of *E. minimus* (Preble, 1908) so that variations in weather may unduly influence this population in comparison with those from latitudes nearer the center of the geographic range of the species.

Marked fluctuations in population size are normally regarded as principally a phenomenon of higher latitudes. The hypothesis proposed in the present study could be applicable to populations in more temperate climates as well as to that at Heart Lake. The short growing season for plants in the "oscillating environment" (Dunbar, 1968) of higher latitudes is probably subject to more variability than those of the progressively more constant meteorological conditions with decreasing latitude. A paucity of plant species at higher latitudes has also been suggested as a factor not conducive to stability in animal populations (MacArthur, 1955; Connell and Orias, 1964; Pianka, 1966). Food supplies thus probably fluctuate to a greater extent at higher latitudes so that the numbers of home ranges available would fluctuate more than at lower latitudes. A greater variation would be expected in the number of animals supported on a predetermined area in the Northwest Territories than in say, coastal California.

CONCLUSIONS

Those questions posed at the beginning of this study have been answered. Chipmunk populations neart Heart Lake did not remain constant but declined from 1967 to 1970 and increased slightly in 1971. Population changes were not synchronous with those of red-backed voles in the same area as voles declined in 1967 to lowest numbers in 1968 and remained virtually constant from 1969 to 1971. Reasons for asynchrony in population fluctuations between the two species were considered to be related to differences in both potential rates of increase and survival rates. Species with dissimilar life histories can thus respond in different ways to common extrinsic factors.

Breeding in *E. minimus* was restricted to a short period in spring soon after emergence from hibernation. Following six weeks of weaning, juveniles emerged from the maternal burrows in mid-July, after which growth was rapid. However, considerable variation was noted in body weights of juveniles in August when heavier chipmunks ("collectors") carried seeds in their cheek pouches while lighter individuals ("non-collectors") did not.

Breeding does not occur until chipmunks have overwintered at least once. The proportion of females that bred remained approximately constant above a threshold which was postulated to be related to the number of home ranges available and breeding increased only when the population level fell below that threshold. The number of suitable home ranges was probably related to climatically-determined food resources as large annual differences were observed in both quantity and quality

(i.e., species available) of berries.

Variability in breeding success was most pronounced in yearlings where only 50% of the females showed evidence of having bred. Breeding yearling females were significantly larger in both body weights and cranial measurements than non-breeding females of the same age. Breeding females in all age classes contributed to full capacity each year as there was no significant change in embryonic contribution and no evidence of mortality during weaning. The percentage of females breeding within each age class increased each year so that the chance of an individual female contributing to the population increased with age.

Survival rates were lower in the first than in the second and third years of life. Only a few individuals from one cohort, which probably had an increased food supply in its first year, survived to four years of age. Mortality did not appear to occur in summer but may have occurred in late fall when individuals without established home ranges were seeking overwintering sites. Earlier studies also suggest that mortality may occur in hibernacula during winter in those individuals with small hoards. The proportion of females increased with age, an adaptation which would increase the reproductive potential of a population in which males were promiscuous.

It was proposed that juvenile "collectors" overwintered to form the heavier breeding portion of the yearling age class and that "non-collectors" either failed to survive or overwintered on marginal home ranges to form non-breeding yearlings. Continued growth throughout summer would provide most non-breeding yearlings with a competitive advantage over the new juvenile cohort for home ranges and they would

reach breeding capacity for the first time at two years of age. The small percentage of two-year-old animals which did not breed would perhaps be sterile or would have failed to establish adequate hom ranges as yearlings and would have survived a second winter on marginal home ranges.

Many theories regarding population regulation were incorporated into the present hypothesis, which must remain largely tentative. Further investigations are necessary before conclusions can be made concerning the validity of this concept.

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APPENDIX I. Total numbers of trap-days in different vegetative associations (see Fig. 1) on live-trapping plots each year.

Plot A: JB = jackpine, some white spruce, plus balsam poplar
TG = tamarack, black spruce plus gravel

Plot B: JW = jackpine, some white spruce
BP = balsam poplar
JA = jackpine, birch, aspen, alder

Plot C: JJ = jackpine, occasional alder and juniper

Year	Plot A		Plot B			Plot C
Association	JB	TG	JW	BP	JA	JJ
1967	4,746	2,254	753	719	953	1,575
1968	9,603	4,097	1,106	1,011	1,308	3,425
1969	11,584	5,616	1,453	1,112	1,760	4,325
1970	8,008	3,932	964	755	1,106	2,825
1971	8,061	3,439	1,010	750	1,115	2,875

APPENDIX II. Chipmunks captured on live-trapping plots.

Sex: M = male; F = female
Date = date of initial capture
Age: A = overwintered once or more; J = juvenile
Reprod = reproductive status at time of first capture.
Males: S = scrotal testes; females: P = pregnant;
L = lactating; E = enlarged nipples

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
1967							
A	3	16.vi	F	53.9	A		18.vi; 21.vi; 22.viii
A	4	16.vi	F	52.6	A	L	18.vi; 21.vi; 24.vi; 25.vi
A	5	17.vi	F	43.5	A		19.vi; 23.vi; 24.vi; 1.vii
A	6	17.vi	F	49.1	A	E	23.vi (dead = 6703A)
A	7	17.vi	F	48.1	A		19.vi; 26.vi; 28.vi; 22.vii; 23.vii; 28.vii
A	9	22.vi	F	45.3	A		28.vi; 6.vii
A	12	23.vi	M	41.5	A		26.vi; 26.vi; 30.vi; 3.vii; 8.vii; 10.vii; 20.vii; 23.vii; 24.vii; 29.vii; 30.vii
A	13	24.vi	F	46.2	A		30.vi; 8.vii
A	14	25.vi	F	50.5	A		(dead = 6703)
A	15	26.vi	M	40.1	A		4.viii
A	16	28.vi	F	52.3	A	E	9.vii; 24.vii; 26.vii
A	18	2.vii	F	41.3	A		26.vii
A	19	3.vii	M	48.2	A		
A	21	11.vii	M	40.0	A		
A	23	12.vii	M	45.8	A		

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
A	24	20.vii	F	17.9	J		24.vii
A	25	20.vii	M	23.9	J		
A	28	22.vii	F	34.3	J		24.vii (dead = 6705A)
A	29	22.vii	M	30.6	J		
A	31	22.vii	F	37.0	J		26.vii; 28.vii; 29.vii
A	32	22.vii	M	31.2	J		
A	36	23.vii	F	31.7	J		25.vii; 25.vii; 26;vii; 26.vii; 27.vii; 28.vii; 28.vii; 29.vii; 30.vii; 31.vii; 1.viii
A	38	24.vii	M	27.9	J		28.vii; 2.viii
A	39	26.vii	M	32.3	J		
A	40	27.vii	F	34.4	J		28.vii; 30.vii; 30.vii; 3.viii; 5.viii; 5.viii; 7.viii; 17.viii
A	41	27.vii	M	32.9	J		1.viii
A	44	29.vii	F	31.4	J		
A	45	30.vii	M	36.4	J		6.viii; 17.viii
A	47	30.vii	M	39.7	J		4.viii; 22.viii
A	48	31.vii	M	56.4	A		14.viii; 17.viii
A	50	31.vii	F	37.0	J		
A	55	1.viii	F	33.0	J		6.viii
A	57	2.viii	F	51.7	A	E	
A	59	2.viii	F	37.2	J		
A	64	4.viii	F	40.3	J		16.viii

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
A	66	4.viii	F	34.8	J		
A	72	15.viii	M	38.5	J		20.viii
A	73	20.viii	M	41.0	J		
B	1	19.v	F	37.9	A		20.v; 21.v; 22.v; 24.v; 24.v; 25.v; 25.v; 27.v; 27.v; 28.v; 28.v; 29.v; 30.v; 30.v; 31.v; 1.vi; 1.vi; 3.vi; 8.vi; 12.vi; 18.vi (dead = 6702)
B	2	22.v	F	47.1	A		
B	8	18.vi	F	50.1	A		21.vi; 29.vi (dead = 6703B)
B	17	2.vii	F	42.3	A		17.vii; 21.vii
B	20	8.vii	M	46.5	A		
B	22	11.vii	M	45.6	A		
B	26	20.vii	M	33.3	J		
B	27	20.vii	M	36.5	J		26.vii; 28.vii
B	30	22.vii	F	36.6	J		24.vii
B	33	22.vii	M	33.2	J		5.viii
B	34	22.vii	M	31.4	J		
B	35	22.vii	M	25.2	J		
B	37	24.vii	F	36.3	J		
B	42	27.vii	F	49.6	A	E	30.vii; 14.viii
B	51	31.vii	F	33.1	J		
B	52	1.viii	M	39.3	J		
B	54	1.viii	M	35.2	J		18.viii; 21.viii

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
B	60	2.viii	F	40.5	J		
B	61	3.viii	M	36.9	J		
B	67	6.viii	M	33.4	J		
B	70	14.viii	M	41.3	J		
C	43	28.vii	M	30.5	J		
C	46	30.vii	F	30.7	J		
C	49	31.vii	F	45.4	A		4.viii
C	53	1.viii	M	47.1	A		(dead = 6708)
C	56	1.viii	M	41.8	J		7.viii
C	58	2.viii	M	46.2	A		
C	62	3.viii	F	33.5	J		
C	63	3.viii	F	42.7	J		18.viii
C	65	4.viii	M	38.7	J		
C	68	6.viii	M	40.5	J		
C	69	6.viii	F	38.3	J		
C	71	14.viii	M	39.7	J		17.viii
1968							
A	72	13.v	M	41.4	A	S	18.v; 19.v; 19.v; 20.v; 21.v; 22.v (dead = 6812)
A	15	21.v	M	36.1	A		
A	73	24.v	M	34.6	A		30.v
A	75	1.vi	M	37.1	A		6.vi; 21.vi; 22.vi; 24.vi; 28.vi; 30.vi; 1.vii; 7.vii

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
A	76	4.vi	M	42.7	A		9.vii
A	77	5.vi	M	39.3	A		26.vi; 28.vi
A	71	18.vi	M	41.2	A		3.vii; 5.vii; 8.vii; 9.vii; 11.vii (dead = 6820)
A	81	9.vii	F	41.1	A		20.vii
A	82	11.vii	F	40.0	A		
A	83	17.vii	M	44.1	A		
A	84	19.vii	F	36.9	J		22.vii; 23.vii
A	85	19.vii	M	30.0	J		27.vii; 28.vii; 28.vii; 29.vii; 1.viii; 5.viii; 6.viii; 9.viii; 10.viii; 12.viii; 15.viii; 4.ix
A	86	19.vii	F	31.5	J		
A	87	19.vii	M	32.2	J		20.vii; 22.vii; 22.vii; 23.vii; 23.vii; 26.vii (dead = 6824)
A	88	20.vii	M	32.6	J		26.vii
A	89	20.vii	M	35.9	J		9.viii; 17.viii; 18.viii; 5.ix; 5.ix; 7.ix; 8.ix; 9.ix; 9.ix; 10.ix; 11.ix
A	90	21.vii	M	28.8	J		
A	91	22.vii	F	39.1	J		
A	96	27.vii	M	29.4	J		6.viii
A	97	27.vii	F	30.0	J		31.vii; 2.viii; 4.viii; 8.viii; 9.viii; 10.viii; 11.viii; 13.viii; 16.viii; 18.viii; 18.viii; 21.viii; 4.ix; 5.ix; 6.ix; 6.ix; 7.ix; 8.ix; 9.ix; 9.ix; 10.ix; 10.ix; 11.ix; 11.ix

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
A	98	31.vii	M	39.8	J		
A	99	31.vii	M	33.8	J		8.viii; 11.viii
A	100	31.vii	M	29.4	J		
A	101	31.vii	M	32.5	J		13.viii; 17.viii; 4.ix (dead = 6844)
A	104	4.viii	M	33.5	J		
A	106	6.viii	F	37.3	J		(dead = 6835)
A	107	7.viii	F	41.9	A		13.viii; 18.viii; 4.ix (dead = 6845)
A	112	10.viii	M	38.9	J		4.ix (dead = 6843)
A	113	11.viii	M	31.2	J		
A	115	13.viii	F	39.4	J		16.viii; 17.viii; 4.ix; 5.ix; 6.ix; 7.ix; 7.ix; 8.ix; 8.ix; 9.ix; 9.ix; 10.ix; 10.ix; 11.ix; 11.ix
A	116	14.viii	F	34.7	J		4.ix; 5.ix; 6.ix; 7.ix; 7.ix; 8.ix; 9.ix; 9.ix; 10.ix; 10.ix; 11.ix; 11.ix; 12.ix (dead = 6846)
A	118	5.ix	M	46.9	J		
B	70	16.v	M	37.1	A		18.v; 19.v; 20.v (dead = 6811)
B	42	22.v	F	57.0	A	P?	29.v; 30.v; 31.v; 1.vi; 2.vi
B	74	24.v	M	38.9	A		18.vi; 25.vi (dead = 6819)
B	54	11.v	M	36.1	A		19.v; 20.v; 7.vi (dead = 6816)
B	78	18.vi	F	45.4	A		

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
B	79	27.vi	M	44.8	A		30.vi; 22.vii
B	80	8.vii	F	39.8	A		
B	92	24.vii	M	27.9	J		
B	93	26.vii	M	35.1	J		21.viii; 11.ix
B	94	27.vii	M	30.9	J		30.vii; 16.viii
B	95	27.vii	M	34.7	J		
B	102	1.viii	M	33.1	J		21.viii
B	103	2.viii	M	34.9	J		7.viii; 8.viii; 11.viii; 12.viii; 15.viii; 16.viii; 18.viii; 18.viii; 19.viii
B	105	5.viii	M	37.2	J		11.viii
B	108	8.viii	M	33.5	J		14.viii; 19.viii; 20.viii
B	110	10.viii	M	34.9	J		16.viii; 17.viii; 21.viii; 9.ix
B	114	12.viii	F	43.8	J		
C	69	10.vii	F	51.1	A	L	27.vii
C	109	9.viii	F	39.2	J		
C	111	10.viii	F	38.2	J		
C	117	18.viii	F	44.7	A		
1969							
A	115	17.v	F	37.0	A		19.v; 20.v; 21.v; 23.v; 23.v; 24.v; 24.v; 25.v (dead = 6919)
A	128	30.vii	M	28.6	J		(dead = 6943)
A	132	3.viii	M	41.8	J		13.viii

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
A	133	4.viii	M	40.2	J		
A	135	8.viii	M	41.8	J		13.viii; 15.viii; 18.viii; 19.viii; 27.viii
A	136	8.viii	F	38.5	J		17.viii
A	139	15.viii	F	35.3	J		(dead = 6957)
A	141	31.viii	M	42.3	A		4.ix; 19.ix (dead = 6965)
A	142	3.ix	M	39.3	J		
B	119	16.v	M	33.4	A		
B	126	28.vii	M	37.3	J		6.viii; 15.viii; 17.viii; 19.viii
B	129	30.vii	M	37.6	J		16.viii; 17.viii; 18.viii (dead = 6958)
B	131	2.viii	F	48.7	A		
B	137	9.viii	F	38.6	J		
B	138	11.viii	M	37.6	J		
B	140	19.viii	M	37.8	J		17.viii; 22.viii
C	56	30.v	M	39.2	A		(dead = 6921)
C	120	12.vi	M	47.5	A		13.vi; 3.ix
C	111	14.vi	F	51.6	A	E	15.vi; 18.vi; 20.vi; 29.vi; 18.vii (dead = 6929)
C	121	18.vii	M	32.7	J		(dead = 6930)
C	122	20.vii	F	37.2	J		19.ix (on Plot B)
C	123	20.vii	F	38.2	J		9.viii
C	20	23.vii	M	43.5	A		18.x

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
C	124	24.vii	F	45.0	A	E	29.vii; 9.viii
C	125	26.vii	F	30.1	J		
C	127	29.vii	M	34.0	J		
C	130	2.viii	M	44.0	J		6.viii; 24.viii; 3.ix; 4.ix; 6.ix; 23.ix (dead = 6966)
C	134	7.viii	M	40.4	J		31.viii; 18.ix
1970							
A	82	12.v	F	42.0	A		15.vii (dead = 7019)
A	143	5.viii	M	29.8	J		(dead = 7044)
A	150	10.viii	M	35.5	J		(dead = 7050)
A	151	10.viii	F	38.1	J		16.viii; 17.viii; 19.viii
A	10	13.viii	M	38.6	J		20.viii; 23.viii; 25.viii; 26.viii
A	156	20.viii	F	40.5	J		
B	138	1.vi	M	53.2	A		11.vi
B	146	6.viii	F	30.4	J		(dead = 7045)
B	147	6.viii	F	30.9	J		(dead = 7046)
B	149	8.viii	M	41.6	J		
B	152	11.viii	M	42.1	J		23.viii; 8.ix (dead = 7066)
B	11	13.viii	F	37.8	J		20.viii
B	153	13.viii	F	44.5	A		
B	154	18.viii	M	40.2	J		25.viii
C	134	10.vii	M	40.2	A		(dead = 7008)

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
C	144	5.viii	F	46.4	A		
C	145	5.viii	M	33.9	J		
C	148	6.viii	M	38.0	J		
1971							
A	158	7.vii	F	39.0	A		
A	157	17.vii	M	27.6	J		7.viii (dead = 7130)
A	159	18.vii	M	41.0	A		
A	160	19.vii	F	44.9	A		
A	162	25.vii	M	31.7	J		
A	163	29.vii	F	39.1	A		(dead = 7120)
A	164	29.vii	M	37.4	J		
A	165	30.vii	M	37.8	J		
A	166	3.viii	F	39.8	J		
A	168	4.viii	M	38.9	J		
A	169	5.viii	M	39.7	J		
A	170	7.viii	M	39.6	J		(dead = 7131)
A	175	18.viii	M	44.8	A		(dead = 7137)
B	161	25.vii	F	48.4	A		
B	167	31.vii	F	39.4	J		
B	171	10.viii	M	39.8	J		(dead = 7133)
B	172	13.viii	M	36.2	J		(dead = 7135)
B	173	17.viii	F	39.1	J		(dead = 7136)

APPENDIX II (Continued)

Plot	No.	Date	Sex	Wt (g)	Age	Reprod	Recapture dates
B	174	18.viii	M	37.6	J		
B	176	22.viii	M	38.3	J		(dead = 7138)
C	144	21.vi	M	53.2	A		7.viii (dead = 7129)

APPENDIX III. Mean body weights (in grams) of overwintered animals autopsied throughout the study

Year	Mean body weight (grams)			
	Total overwintered animals	Females	Females with placentae and embryos removed	Males
1967	47.66	48.89	48.89	44.80
1968	43.11	45.96	45.88	39.89
1969	42.77	44.31	44.14	40.76
1970	43.79	47.38	47.25	39.91
1971	44.89	46.02	45.87	44.08

APPENDIX IV. Protocol of chipmunks in autopsied samples. Age (in years) was determined by histological examination of dentaries and refers to the summer of each collecting period.

Veg = vegetative association (as in Appendix I) in which each animal was collected: C-XX = captive animals plus vegetation at initial capture point.
Reprod: Males - A = abdominal testes; I = inguinal testes; S = scrotal testes; Females - B = breeding; N = non-breeding
Stomach: + = contained food
C.P. = cheek pouches: + contained seeds

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
					1967			
Juveniles								
6703F	15.vii.67	M	28.4	-	A			Born in captivity
6703G	15.vii.67	F	29.0	-				Born in captivity
6703H	15.vii.67	F	27.0	-	-			Born in captivity
6705	20.vii.67	M	29.5	JW	A-I			
6705A	23.vii.67	F	34.3	JB				= No. 28
6707	26.vii.67	M	29.6	JW	A			
6708A	5.viii.67	M	33.2	-	A			Born in captivity
6709	17.viii.67	F	32.0	JW				
6710	6.x.67	F	40.8	C-JW				
6711	22.x.67	F	42.0	C-JA				
6712	15.xi.67	M	38.1	C-JA	A			
6713	20.xi.67	M	37.9	C-JJ	A			
6714	30.xi.67	M	44.0	C-BP	A			
6716	27.xii.67	M	36.2	C-JJ	I			Captive since 29.vii.67

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
6717	27.xii.67	M	41.7	C-JB	I			Captive since 4.viii.67
6718	8.ii.68	F	34.1	C-JA				Captive since 23.viii.67
6719	8.iii.68	F	41.0	C-BP				Captive since 12.viii.67
6720	19.iii.68	M	24.1	C-JW				Captive since 17.viii.67
6721	2.iv.68	F	49.6	C-JW				Captive since 29.viii.67
Yearlings								
6702	18.vi.67	F	37.0	BP	NB	+		= No. 1
6703	25.vi.67	F	50.5	JB	B			= No. 14
6703A	23.vi.67	F	49.1	JB	B			= No. 6
6703C	1.vii.67	M	46.8	BP	I	+	+	
6703D	1.vii.67	M	49.5	BP	I			
6708	1.viii.67	M	47.1	JJ	A			= No. 53
6715	5.xii.67	F	50.9	C-JJ	NB			Captive since 20.vii.67
Two-year-olds								
6701	15.vi.67	M	38.1	JW	I	+		
6704	19.vii.67	F	47.8	JA	B			
Three-year-olds								
6703B	29.vi.67	F	50.1	JA	NB			= No. 8

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Three-year-olds (continued)								
6703E	10.vii.67	F	56.2	JJ	B			
6706	24.vii.67	F	51.5	JA	B	+		
				1968				
Juveniles								
6803	6.1.69	M	44.5	C-JA	I			Captive since 8.viii.68
6804	14.ii.69	M	40.2	C-JJ	S			Captive since 4.viii.68
6806	11.iii.69	F	41.2	C-JW				Captive since 14.viii.68
6807	11.iii.69	F	30.8	C-BP				Captive since 19.viii.68
6808	18.iii.69	F	30.6	C-JW				Captive since 19.viii.68
6821	22.vii.68	M	24.1	JJ	A			
6822	22.vii.68	F	26.1	JA				
6824	26.vii.68	M	32.4	JB	A			= No. 87
6825	27.vii.68	M	28.8	JB	A			
6826	28.vii.68	M	35.0	BP	A			
6827	29.vii.68	M	30.1	JW	A-I			
6829	3.viii.68	M	37.9	BP	A			
6830	4.viii.68	F	37.5	JJ				
6834	5.viii.68	M	40.8	JW	I	+	+	

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Juveniles (continued)								
6835	6.viii.68	F	37.3	JB				= No. 106
6836	12.viii.68	F	33.8	JJ				
6837	12.viii.68	M	27.4	JA	A-I			
6839	18.viii.68	M	42.3	JA	A-I			
6840	19.viii.68	M	34.1	JB	A			
6841	23.viii.68	F	41.8	JJ				
6842	27.viii.68	M	38.7	BP	A-I			
6843	4.ix.68	M	39.6	JB	A			= No. 112
6844	4.ix.68	M	42.0	JW	A-I			= No. 101
6846	12.ix.68	F	33.8	JW				= No. 116
Yearlings								
6802	30.xii.68	F	34.3	C-JW	NB			Captive since 18.vi.68
6811	20.v.68	M	37.0	JW	I-S			= No. 70
6812	22.v.68	M	41.4	JB	S			= No. 72
6814	25.v.68	F	41.7	BP	NB	+		
6816	7.vi.68	M	36.6	JB	I	+		= No. 54
6817	10.vi.68	M	47.8	JJ	I-S	+	+	
6818	13.vi.68	F	54.1	BP	B	+		
6820	11.vii.68	M	46.4	JB	I			= No. 71
6823	24.vii.68	M	35.7	JJ	A-I			

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
6828	2.viii.68	F	41.7	JJ	NB			
6833	5.viii.68	F	42.1	JA	NB	+		
6838	17.viii.68	M	33.9	JA	I			
6845	4.ix.68	F	41.9	JW	NB			= No. 107
Two-year-olds								
6801	28.xii.68	M	32.4	C-JA				Captive since 24.vii.68
6805	26.ii.69	M	47.2	C-JA	S			Captive since 30.vi.68
6809	12.iv.69	F	41.0	C-JW	B (?)			Captive since 16.vii.68
6810	13.v.69	M	39.2	C-JA	S			Captive since 24.viii.68
6813	24.v.68	F	58.0	JJ	B	+		
6815	7.vi.68	F	37.3	JA	B	+		
6819	25.vi.68	M	40.3	JW	I	+		= No. 74
6831	4.viii.68	F	49.2	JW	B			
Three-year-olds								
6832	4.viii.68	F	47.8	JW	B			
				1969				
Juveniles								
6930	18.vii.69	M	32.7	JA	A			= No. 121
6932	19.vii.69	F	31.5	JW		+		

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Juveniles (continued)								
6933	19.vii.69	M	31.4	JJ	A			
6934	20.vii.69	M	34.4	JW	A	+		
6935	20.vii.69	F	35.5	TG		+		
6936	20.vii.69	F	36.0	JJ		+	+	
6938	21.vii.69	F	29.8	JA				
6939	23.vii.69	F	35.5	JW		+	+	
6941	27.vii.69	M	31.7	JA	I	+		
6942	28.vii.69	M	?	BP	A-I	+		Body mangled
6943	30.vii.69	M	28.6	JB	A-I			= No. 128
6944	31.vii.69	M	39.5	JJ	A-I			
6945	1.viii.69	F	37.1	JW		+	+	
6946	2.viii.69	M	38.2	JB	A	+		
6947	4.viii.69	M	39.5	JW	A-I	+	+	
6948	9.viii.69	F	47.3	JJ		+	+	
6950	10.viii.69	M	42.4	BP	I	+		
6951	11.viii.69	M	41.6	JW	A	+		
6952	14.viii.69	M	43.5	JJ	A-I	+		
6953	14.viii.69	M	45.2	TG	I	+		
6954	15.viii.69	M	43.0	JJ	A-I	+	+	
6955	15.viii.69	M	44.3	JJ	A	+	+	
6956	16.viii.69	F	38.1	JJ		+	+	

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Juveniles (continued)								
6957	17.viii.69	F	35.3	JA				= No. 139
6958	18.viii.69	M	45.5	JA	A	+	+	= No. 129
6060	19.viii.69	F	46.5	TG		+		
6961	20.viii.69	M	43.5	JJ	A	+		
6962	24.viii.69	M	44.5	JW	A	+		
6963	4.ix.69	F	35.2	JA				
6964	18.ix.69	F	44.5	JW		+		
6966	23.ix.69	M	38.0	JJ	I-A			= No. 130
6967	10.x.69	F	49.3	JW				
6968	13.x.69	F	33.6	JB				
6969	14.xi.69	F	35.0	C-JB				Captive since 24.viii.69
6970	12.i.70	M	30.4	C-JW				Captive since 30.viii.69
6971	12.i.70	F	28.2	C-JW				Captive since 27.viii.69
6974	8.ii.70	F	28.2	C-JW				Captive since 10.ix.69
6975	13.ii.70	M	31.3	C-JJ	S			Captive since 4.ix.69
6976	15.ii.70	F	35.4	C-BP				Captive since 14.vii.69
Yearlings								
6901	26.iv.69	M	35.7	BP	I-S	+		

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Yearlings (continued)								
6902	26.iv.69	F	29.2	JJ	NB	+	+	
6904	1.v.69	M	37.5	JA	S			
6906	6.v.69	F	45.0	JB	B	+	+	
6907	7.v.69	M	40.0	BP	I	+		
6908	7.v.69	F	38.6	JA	NB	+		
6913	14.v.69	F	46.6	JW	B	+		
6914	15.v.69	F	47.7	JJ	B	+		
6917	20.v.69	F	52.0	JW	B	+		
6918	24.v.69	M	44.2	JJ	S-I	+		
6919	25.v.69	F	32.3	JB	NB			= No. 115
6920	27.v.69	F	50.0	JA	B	+		
6922	2.vi.69	M	42.0	JJ	I-A	+	+	
6924	13.vi.69	M	42.4	BP	I	+		
6925	13.vi.69	M	46.6	JW	S-I	+		
6926	20.vi.69	M	45.3	JA	A-I	+		
6928	27.vi.69	M	35.1	JW	I			
6929	18.vii.69	F	44.3	JJ	B	+		= No. 111
6931	18.vii.69	F	42.4	BP	NB	+	+	
6940	26.vii.69	M	46.4	JW	I	+	+	
6965	19.ix.69	M	37.5	JA	I-A			= No. 141
6972	12.i.70	F	34.2	C-JB	NB			Captive since 2.ix.69

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Two-year-olds								
69001	26.iv.69	M	42.7	JB	S	+		
6905	5.v.69	M	42.7	JB	S	+		
6909	8.v.69	F	48.5	JW	B	+	+	
6911	10.v.69	M	44.1	JW	S	+		
6915	17.v.69	M	45.6	JW	S	+		
6916	20.v.69	F	57.0	JJ	B	+		
6917B	22.v.69	F	38.8	JW	NB			
6917C	22.v.69	F	33.6	JW	NB			
6921	30.v.69	M	39.2	JA	S-I			= No. 56
6923	5.vi.69	F	50.9	JJ	B	+		
6949	9.viii.69	M	38.5	JW	A-I			
6973	12.i.70	F	32.0	C-JW	B			Captive since 17.vii.69
Three-year-olds								
6903	28.iv.69	F	46.0	JJ	B	+		
6910	9.v.69	F	37.6	JJ	B			
6912	12.v.69	F	47.3	JA	B	+		
6917A	21.v.69	M	33.1	JA	I			
6927	21.vi.69	F	59.5	JW	B	+		
6937	21.vii.69	F	45.5	JJ	B	+	+	
6959	19.viii.69	M	38.5	JW	I			

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
					1970			
Juveniles								
7015	11.vii.70	M	20.7	BP	A	+		
7016	12.vii.70	F	32.6	JA		+		
7018	14.vii.70	F	22.7	JW		+		
7022	15.vii.70	F	22.4	BP		+		
7023	17.vii.70	F	39.3	JB		+		
7024	18.vii.70	M	34.6	JW	A-I	+		
7025	19.vii.70	M	28.2	JJ	A-I	+		
7026	19.vii.70	M	27.7	JA	A			
7027	19.vii.70	M	29.3	JW	A			
7028	19.vii.70	M	34.2	JB	A-I			
7029	20.vii.70	F	36.0	JW		+	+	
7030	20.vii.70	F	34.6	BP				
7031	21.vii.70	M	36.1	JW	A-I			
7032	21.vii.70	F	31.2	JJ				
7033	21.vii.70	F	30.4	JA				
7035	28.vii.70	F	38.2	JW		+	+	
7036	29.vii.70	M	31.0	JW	A			
7037	30.vii.70	F	44.4	JA		+		
7038	30.vii.70	F	38.2	JA		+	+	
7039	31.vii.70	M	30.2	JB	A-I			

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Juveniles (continued)								
7040	1.viii.70	F	37.3	JA		+		
7041	3.viii.70	F	38.8	JJ		+	+	
7042	4.viii.70	M	36.5	JW				
7043	4.viii.70	M	38.4	JJ	A-I			
7044	5.viii.70	M	29.8	JB	A			= No. 143
7045	6.viii.70	F	30.4	JA				= No. 146
7046	6.viii.70	F	30.9	BP				= No. 147
7048	9.viii.70	M	41.6	JJ	A-I	+		
7050	10.viii.70	M	35.5	JB	A-I			= No. 150
7051	11.viii.70	F	39.1	JW		+	+	
7053	13.viii.70	F	45.0	JA		+		
7054	19.viii.70	M	38.5	JA		+	+	
7055	20.viii.70	F	39.0	JW				
7056	21.viii.70	M	36.7	JJ	A			
7057	22.viii.70	M	44.3	JJ	I	+		
7058	23.viii.70	M	43.1	JB	I	+	+	
7059	23.viii.70	M	33.1	JW	A			
7062	24.viii.70	F	48.7	JJ		+	+	
7064	11.ix.70	M	41.3	JB		+	+	
7065	12.ix.70	F	46.6	JB		+		
7066	8.x.70	M	45.5	BP		+		= No. 152

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Yearlings								
7001	5.v.70	M	40.5	BP	I-S	+		
7003	5.v.70	M	41.1	JA	I-S	+		
7006	24.v.70	F	44.3	JB	B	+		
7007	8.vi.70	F	50.2	JA	B	+		
7008	10.vi.70	M	35.4	JJ	I			= No. 134
7011	18.vi.70	M	32.6	JA	I			
7013	6.vii.70	F	49.1	JB	B	+		
7020	15.vii.70	M	47.0	JA	A-I	+	+	
7021	15.vii.70	M	40.2	JJ	I	+		
7034	25.vii.70	M	45.5	JJ	I	+		
7047	9.vii.70	M	38.5	JW	I	+		
7054A	20.viii.70	M	40.0	JA	I-A	+	+	
7060	23.viii.70	M	38.5	C-JA	I			Captive since 20.vii.70
Two-year-olds								
7002	5.v.70	M	38.4	JB	S	+		
7005	11.v.70	F	54.1	JJ	B	+		
7009	18.vi.70	M	40.2	JW	I			
7010	18.vi.70	F	32.2	JJ	B			
7012	5.vii.70	F	50.0	JJ	NB	+		
7049	7.viii.70	F	50.5	JW	B	+		

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Two-year-olds (continued)								
7063	27.viii.70	F	45.2	JW	NB	+	+	
Three-year-olds								
7017	12.vii.70	F	45.5	JB	B	+		
7052	13.vii.70	F	47.8	JA	B	+	+	
Four-year-olds								
7004	6.v.70	M	39.5	JW	S	+		
7014	6.vii.70	F	55.4	JJ	B	+		
7019	15.vii.70	F	45.0	JB	B			= No. 82
7061	27.viii.70	F	46.6	JB	B			
				1971				
Juveniles								
7122	26.vii.71	M	38.1	JB	A	+	+	Skull lost - not aged
7123	26.vii.71	F	32.4	JB	A	+	+	Skull lost - not aged
7125	26.vii.71	M	38.4	JB	A	+	+	Skull lost - not aged
7126	27.vii.71	M	41.2	JW	I	+	+	
7127	29.vii.71	M	39.1	JB	I	+	+	= No. 163
7128	4.viii.71	F	43.6	JW		+	+	
7130	7.viii.71	F	36.2	JA				= No. 157
7131	8.viii.71	M	39.6	JB	I			= No. 170

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Juveniles (continued)								
7132	8.viii.71	M	39.2	JA	I	+		
7133	10.viii.71	M	39.8	JW	A-I			= No. 171
7134	12.viii.71	M	40.1	JJ	I	+		
7135	14.viii.71	M	36.2	BP	I			= No. 172
7136	16.viii.71	F	39.1	JA				= No. 173
7138	22.viii.71	M	38.3	JW	I	+		= No. 176
Yearlings								
7101	19.iv.71	M	42.4	JJ	S			
7102	19.iv.71	F	42.3	JJ	B			
7103	29.iv.71	M	43.2	JB	S	+		
7104	30.iv.71	M	44.6	JA	S			
7106	7.v.71	M	48.0	JA	S	+		
7108	10.v.71	F	41.6	JJ	NB	+	+	
7112	14.v.71	M	36.1	JW	I-A			
7113	17.v.71	F	42.6	JJ	B			
7114	22.v.71	M	48.0	JJ	S-I	+		
7116	1.vi.71	M	46.7	BP	S-I	+		
7117	2.vi.71	M	55.3	JW	S-I	+		
7119	17.vi.71	M	41.6	JW	I			
7120	19.vi.71	F	40.1	BP	NB			
7121	27.vi.71	F	56.7	JA	B	+		

APPENDIX IV (Continued)

No.	Date collected	Sex	Wt (g)	Veg	Reprod	Stomach	C.P.	Comments
Yearlings (continued)								
7131	18.viii.71	M	44.8	JB	I			= No. 175
7139	24.viii.71	F	46.3	JA	NB	+		
Two-year-olds								
7105	6.v.71	M	40.1	JB	S	+		
7109	11.v.71	M	40.6	JA	S	+		
7110	11.v.71	F	36.5	JJ	B	+	+	
7115	30.v.71	F	61.5	JB	B	+		
Three-year-olds								
7107	7.v.71	F	41.2	JW	B			
7111	12.v.71	M	43.1	JW	I	+		
7118	4.vi.71	F	51.7	JJ	B	+		
7129	4.viii.71	F	42.3	JJ	B			= No. 144
Adult of unknown age								
7124	26.vii.71	F	49.8	JB	B	+	+	Skull lost

APPENDIX V. Means of four cranial measurements (in mm) for different age classes and reproductive criteria.

TL = total length; ZB = zygomatic breadth; ONL = orbitonasal length; IOB = interorbital breadth; B = breeding; NB = non-breeding; N = sample size

Age (years)	Sex	Reproductive status	N	TL	ZB	ONL	IOB
3	♀ + ♂	B + NB	15	32.86	18.43	31.81	7.19
2	♀ + ♂	B + NB	32	32.85	18.56	31.80	7.26
2	♀	B + NB	29	32.91	18.60	31.90	7.32
1	♀ + ♂	B + NB	68	32.72	18.36	31.59	7.06
1	♀	B	15	33.01	18.51	31.95	7.17
1	♀	NB	14	32.48	18.26	31.34	6.91
Juvenile	♀ + ♂	NB	124	32.10	17.84	30.79	6.84